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A Review of the Literature  
on the  
Spruce Budworm  
*Choristoneura fumiferana* (Clemens)

by  
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3 A REVIEW OF THE LITERATURE

ON THE

SPRUCE BUDWORM, CHORISTONEURA FUMIFERANA (CLEMENS) //

by

MELVIN E. <sup>2</sup>MCKNIGHT

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## PREFACE

The spruce budworm is one of the most important forest insect pests of North America. Investigations of its biology, ecology, and control have been in progress for over 50 years. A review of the literature on spruce budworm in the United States and Canada was completed by the author in 1963 to aid in problem selection at the Rocky Mountain Forest and Range Experiment Station.

Participants in the Spruce Budworm Workshop at Ogden, Utah, February 8-11, 1965, recommended that the literature review be mimeographed and distributed to U.S. Forest Service Experiment Stations and Regions concerned with the spruce budworm problem for their review and use.

The text has not been brought up to date since it was written in February 1963. The "References Not Cited" section includes: (1) titles that appeared prior to 1963 but not reviewed in the text, and (2) titles which have appeared after the attached draft was written. The users of this review draft are urged to inform the author before January 1, 1966, of omissions of published works. Corrections and suggestions for the improvement of the text will be welcome. Publication of the review is planned for 1967.

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Date

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M. E. McKnight



A REVIEW OF THE LITERATURE  
ON THE SPRUCE BUDWORM, CHORISTONEURA FUMIFERANA (CLEMENS)

by

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TAXONOMY

The spruce budworm is a leaf-roller of the family Tortricidae.  
It was recently redescribed by Freeman (1958) in a revision of the  
subfamily Archipinae. The subfamily consists of 72 described species,  
and of these, the spruce budworm and a closely allied species, the  
jack-pine budworm, are the most destructive.

TAXONOMIC HISTORY

In a paper preparatory to the revision of the Archipinae and in  
which he named Choristoneura pinus Free., the jack-pine budworm,  
Freeman (1953) reviewed the taxonomic history of the two species.

The spruce budworm was named by Clemens in 1865 from specimens  
collected in Virginia. In 1890, Packard described damage caused by  
the insect to the spruce and balsam fir in Maine during the late  
19th century. Packard referred to the insect as Tortrix fumiferana  
Clemens. In 1869, Robinson described dark variants under the name  
Tortrix nigridia and based his description on specimens collected in  
Ohio, Pennsylvania, and Massachusetts. In 1913, Meyrick placed the

species in the genus Harmologa Myr., proposed by him for a group of primitive tortricid species from New Zealand. Forbes, in 1923, followed this system. Since that time, the species has been assigned to either Archips Hbn. or Cacoecia Hbn. by economic entomologists and taxonomists. Freeman (1947b) transferred the spruce budworm from Archips Hbn. to the genus Choristoneura Lederer.

#### THE C. FUMIFERANA-C. PINUS SEPARATION

Graham (1935) was the first to point out that the form of budworm feeding on pine was biologically distinct from that form feeding on spruce and balsam fir. He suggested that they be considered specifically distinct. Brown and MacKay (1943) asserted that the jack-pine budworm should be designated a subspecies, if not a separate and distinct species. They presented as evidence differences in size, wing coloration, geographical distribution, host relationships, life cycle dates, and male genitalia.

MacKay (1953) studied the larvae of both species and found structural differences to occur only in the head. The head capsule of pinus is usually larger than that of fumiferana and its length greater, in relation to its width. Also, late instar larvae of fumiferana usually have dark heads and light prothoracic shields; whereas, those of pinus usually have light heads and dark prothoracic shields. Early instar larvae of fumiferana and pinus have heads and prothoracic shields of about the same color, and these characters cannot be used to separate the species.

Cox (1953) demonstrated that the postclypeal index could be used to separate the two closely allied species. The postclypeal

index was defined as L/W, the width of the postclypeus and the length of the median dorsal line from the anterior margin of the postclypeus to the termination of the adfrontal sutures. Cox also analyzed the frequency distribution of the uncus widths of 100 adult males of each species.

The morphological differences between the pupae and egg masses were described by Campbell (Campbell, I. M., 1953). The eggs of fumiferana were laid in two to four rows, with an average of 19 eggs per mass. Balsam fir and spruce were preferred hosts. The eggs of pinus were always laid in two rows with an average of 37 eggs per mass and jack-pine was the preferred host.

Campbell reported that the color of newly formed male pupae of pinus is yellow and female pupae are green. The pupae of both sexes of fumiferana are initially yellowish to blue-green. Stehr (1959) presented evidence that this is a valid separation. C. pinus was found to be sex-dimorphic but not polymorphic as was fumiferana.

Freeman (1958) stated that the two species will not hybridize in nature. They will, however, hybridize readily in captivity. The mechanisms to which the integrity of the species has been attributed are ecological, temporal, and sexual isolation. In 1952, a localized breakdown of the temporal barrier provided Smith (1954) an opportunity to evaluate the relative contributions of the three mechanisms to complete reproductive isolation. In the presence of larval and adult ecological isolation and in the absence of adult temporal isolation, successful matings still did not materialize. It was concluded that sexual isolation is the component of reproductive isolation, making the two species mutually exclusive genetic systems.



THE STATUS OF THE SPRUCE BUDWORM IN  
WESTERN UNITED STATES AND CANADA

Populations of C. fumiferana from British Columbia south to California and New Mexico are described by Freeman (1958) as being extremely variable, particularly in wing maculation and color. Some individuals are almost indistinguishable from the reddish individuals of pinus; yet others resemble the gray variants of eastern fumiferana. Intermediates in color also exist. The width of the subapical portion of the uncus lies between the modes for the two eastern forms of budworm.

Freeman presented three speculations concerning the populations of western budworm:

1. They may represent one or more distinct, highly variable species indigenous to the mountainous regions of western United States and Canada.
2. They may be cordilleran subspecies of either or both of the eastern species.
3. They may represent natural hybrids between the two eastern species.

The study of hemolymph polymorphism cited earlier (Stehr, 1959) showed that the western forms of the budworm are certainly more closely related to the eastern C. fumiferana than to C. pinus. They share with the eastern form all the alleles involved in the blue pigment polymorphism. Thus, Freeman's second hypothesis may be a valid assumption.



Freeman (1958) described an unusual form that occurs in Colorado and California. The general color of the forewing is light ochreous with suffused darker ochreous spots. Anatomically it appears allied to the western budworm complex. On the basis of the small amount of material examined by him, Freeman suggested that this form may represent a distinct species.

#### TWO-YEAR CYCLE BUDWORM

Mathers (1932) first described the life history of a form of budworm requiring 2 years to complete a generation in British Columbia. Third instar larvae cease their activity in July of their first feeding season and spin their second hibernacula (the first having been formed the previous fall). The following May the larvae emerge, continue feeding, and complete development.

Shepherd's (1961) studies of habitat temperature correlated with developmental rates indicated that in most years the summer season is too short and too cool for 1-year cycle budworm to succeed. Apparently cool temperatures are responsible for the selection and maintenance of populations with a second diapause at the higher elevations of Alberta and British Columbia.

#### DAMAGE

##### DIRECT EFFECTS OF BUDWORM DEFOLIATION

The characteristics and effects of defoliation of spruce by the European spruce sawfly (Gilpinia hercyniae) and the spruce budworm were compared by Reeks and Barter (1951). The sawfly prefers old foliage, and the budworm prefers new foliage. The sawfly causes cessation of bud growth by exhausting the growing power of branches

by gradual destruction of the needles. No buds are killed directly, and no adventitious buds arise. The budworm kills buds and young shoots directly by feeding and adventitious buds are forced. Some feeding on old growth occurs after new growth has been consumed. The budworm kills the tree from the top downwards, the sawfly from the bottom upwards.

#### DATING OUTBREAKS BY ANNUAL RINGS

Craighead (1923) pointed out that loss of needles from the host tree due to defoliation by the spruce budworm was reflected immediately by reduction of the current annual ring. This phenomenon has been used to date the occurrence of spruce budworm outbreaks. Mott et al. (1957) studied, in detail, the effects of defoliation on radial growth at different locations in the tree stem.

Injuries caused by certain frosts can also produce characteristic "frost rings" (Bailey 1925). In eastern Canada, these rings were found in balsam fir, alder, hazel, birch, cherry, and mountain ash. By cross-checking the frost rings in budworm hosts with those of other vegetation in the area, budworm outbreaks may be more accurately dated.

During an outbreak in northwestern Ontario, defoliation was recorded yearly in certain stands from the beginning of the infestation (Blais 1958a). Radial growth measurements were obtained from increment cores taken at breast height from white spruce and balsam fir of merchantable size. The first year of radial growth suppression was calculated by comparing the growth of the spruce and fir with that

of jack-pine and red pine. This generally occurred, at the earliest, in the second year and, at the latest, in the fourth year of severe defoliation.

Chent (1958b) found that satisfactory histories of spruce budworm outbreaks were recorded by damage to the main axis of seedlings caused by feeding of late instar larvae that dropped from the overstory.

#### LOSS OF INCREMENT

The characteristic increment reduction is a distinct loss to the forest manager. Craighead (1925) observed that in trees that survived budworm attack the diameter growth for the 10-year period following the first year of feeding was only about one-half that of the preceding 10 years.

McLintock (1955) studied spruce budworm damage during a heavy outbreak in southwestern Quebec from 1944 to 1950. Increment cores from more than 100 trees showed a drop in increment in all trees beginning in 1 to 6 years, and most marked in 5 to 6 years, after the first defoliation. This drop continued for at least 3 years after defoliation ceased.

#### EFFECT OF DEFOLIATION ON NEEDLE COMPLEMENT

Cole, studying the spruce budworm population-damage relationships in Douglas-fir and alpine fir in Idaho, observed that on a plot which had been infested with budworm for 10 years, there was approximately one-half the number of needles per inch of twig growth for 6 years, but almost twice the inches of twig growth for the same period, compared to a plot which had been infested only 1 year (Cole 1958). His studies suggested that defoliation by the

budworm does not appear to greatly affect needle complement (Cole 1959).

#### ROOTLET MORTALITY IN BALSAM FIR

Swaine et al. (1924) reported that during the outbreak of 1912 to 1920 in the New Brunswick area, all rootlets and roots less than 2 millimeters in diameter were dead 6 months prior to the death of severely damaged trees. Redmond (1959), by sequential sampling, found that when the defoliation of new shoots was greater than 70 percent, rootlet mortality was greater than 30 percent. When the loss of current growth reached 100 percent, rootlet mortality soon exceeded 75 percent. When the defoliation of young trees diminished or ceased, rootlets were immediately regenerated, but the trees were unable to survive a recurrence of defoliation severe enough to kill these new rootlets. Mature trees were less able, and overmature trees were unable, to regenerate new rootlets after 4 or 5 successive years of total defoliation of new shoots.

Stillwell (1960) reported progress on a study, initiated in 1957, to determine the relationship between rootlet recovery and foliage recovery. In 1950, 20 percent of the current foliage was lost, 40 percent in 1951, and 100 percent from 1952 to 1955; but very little after that year. Rootlet samples were taken in 1957, 1958, and 1959, and the degree of mortality was determined using the sequential sampling plan devised by Redmond (1959). By 1959, rootlet recovery in 43 of 47 trees appeared to be normal. It was concluded that rootlet recovery lagged behind foliage recovery by 3 years.

## TREE MORTALITY

During an outbreak that occurred in the early 1900's in Quebec, Ontario, New Brunswick, and Maine, Craighead (1923) observed that all trees receiving 75- to 100-percent defoliation died 1 to 2 years later. No trees receiving less than 25-percent defoliation died.

In the Lake Nipigon Region, Belyea (1952b) found that balsam fir mortality commenced in the fifth year of severe defoliation by the budworm. Mortality became complete, or nearly complete, 8 years after the first year of severe defoliation.

In the outbreak that occurred in southwestern Quebec between 1944 and 1950, the first mortality was observed in 1948 and the first heavy mortality in 1949 (McLintock 1955). In the overstory, there was little difference in mortality in the d.b.h. classes 4 to 5 and 6 to 8 inches, but from 9 inches upwards, mortality was about 10 percent higher each year than in classes below 9 inches. Dominant and intermediate trees sustained heavier losses than overtopped (but not suppressed) trees. Mortality was heavier among trees suffering heavy than among those suffering medium or light defoliation, and in trees with short crowns than in those with larger crowns. No consistent relationship was found between site quality and mortality, but there appeared to be higher mortality on poorly drained sites.

Top-killing is a characteristic of prolonged outbreaks. Schmeige (1961) reported top-killing as high as 78 percent in some areas in the Lake States.



Silver (1960) commented on the ability of Douglas-fir trees to sustain severe defoliation and remain alive. In an infestation in British Columbia, numerous trees had all of their buds killed, lost over 90 percent of their needles, and yet no trees on the study plots were killed. Top-kill was common, but usually only 1 or a few years terminal growth was killed back. Branch tips were killed, but heavy adventitious budding made recovery rapid. Radial growth began to improve the year after the first year of light defoliation.

#### EFFECTS ON REGENERATION

The spruce budworm was observed by Tripp (1950) to feed in and on white spruce cones and in preference to foliage. LeBarron (1944) reported that insects were the chief cause of early mortality of jack-pine and black spruce seedlings. The spruce budworm was observed to feed on the tops of the seedlings.

Ghent et al. (1957) concluded that whatever trends of forest succession develop after a spruce budworm outbreak do so on a regional basis. If the site and climate are favorable, either spruce or balsam fir may increase in proportion following an outbreak. Apparently neither has greater competitive abilities in all circumstances.

An early effect of defoliation in balsam fir is the cessation of female flower production (Ghent 1958b). During an outbreak, seedling release does not take place because of feeding by larvae that drop from the overstory. Seedling height increases immediately following the period of peak budworm populations and when overstory mortality begins.

## EFFECT OF FOREST COMPOSITION

Craighead (1925) stated that in hardwood types the immunity of softwoods was proportional to the protection of the hardwood overstory. The percentage mortality of dominant softwoods in mixed stands was as high as in pure softwood stands. Turner (1952) found that where fir was of intermediate height, fir mortality decreased with increasing proportions of hardwoods. Where fir was understory, fir mortality increased with increasing proportions of hardwoods; the fir possibly being more susceptible with increased shade. Where fir was codominant, the proportions of hardwood did not affect fir mortality. In general, increasing fir mortality accompanied increasing relative height of fir. Within all localities of generally high fir mortality and in most of the broad cover types studied, the percentage mortality of fir increased with the basal area of fir per acre.

## DETERIORATION OF DEFOLIATED TREES

The role of insects.--Belyea (1952a) found the following species of insects attacking severely weakened or newly dead balsam fir trees:

### Order COLEOPTERA

#### Family Cerambycidae

Monochamus scutellatus Say--the white-spotted sawyer beetle

Monochamus marmorator Kby.--the balsam sawyer beetle

Tetropium cinnamopterum Kby.--the four-eyed spruce borer

#### Family Curculionidae

Pissodes dubius Rand.--the balsam weevil

#### Family Scolytidae

Pityokteines sparsus Lec.--the balsam bark beetle

Trypodendron bivittatum Kby.--the spruce ambrosia beetle

#### Family Melandryidae

Serropalpus substriatus Hald.

Order HYMENOPTERA

Family Siricidae

Sirex cyaneus F.

Sirex sp. (noctilio group)

Urocerus albicornis F.

Of these, only two, Pityokteines sparsus and Monochamus scutellatus, were abundant. They were observed to attack the trees before death but their activity was such that no damage was done before the tree died (Belyea 1952b).

Pathological deterioration.--On the Green River Watershed, balsam fir with forked tops, marked crooks, and slight sweeps or crooks were felled and dissected to relate the size of buried leaders to the extent of decay resulting from the 1912 to 1920 budworm outbreak (Stillwell 1956). All of the trees with forked tops and marked crooks, but none of the trees with slight sweeps or crooks showed decay entering through budworm injury. Buried leaders of  $\frac{1}{2}$ -inch diameter or larger were always seats of origin for decay. Those smaller and younger were not.

Basham and Belyea (1960) found the general pattern of deterioration to consist of a relatively sudden invasion by insects at or near the time of apparent tree death. This was followed by a more gradual fungal invasion which completely replaced the insects after 2 years. Evidence indicated that bark beetles, sawyer beetles, and weevils carry deteriorating fungi from dead balsam fir to dying or newly killed trees and that the development of sap rot is related to sawyer beetle activity.

Stillwell (1962) reported that the rate of deterioration by decay is more rapid in balsam fir trees killed by insects than in



trees killed by fire or windthrow. Two years after death decay caused mainly by Stereum chailletii penetrates one-half inch but is not present in windthrown or fire-killed trees. Wood wasps, Sirex juvencus (L.) and Urocerus spp., may introduce S. chailletii into the sapwood of trees weakened by budworm defoliation. Another species, Xeris spectrum (L.) also oviposits in balsam fir but lacks the specialized sacs in which the fungal strands of S. chailletii are carried and does not transmit the organism.

Moisture content is another factor influencing the rate of deterioration. In contrast to fire-killed and windthrown trees, trees killed by the budworm remain standing, the bark loosens slowly, and the moisture content remains high enough for decay to develop.

#### BIOLOGY

##### ANATOMY AND MORPHOLOGY

The embryonic development of the spruce budworm was described and compared with that of other Lepidoptera by Stairs (1960). He described the techniques of preparation, staining, and embedding budworm eggs. At a rearing temperature of 25° C., the larvae emerged from the eggs at 150 hours.

Descriptions of the larva, pupae, and egg masses of the spruce budworm resulted from comparisons with C. pinus during the separation of the species. These descriptions have been cited earlier (MacKay 1953; Campbell, I.M., 1953). The external anatomy of spruce budworm moths was described by Freeman (1947a) in preparation for his taxonomic revision of the Archipinae.

## PHYSIOLOGY

The pH of the blood and gut contents of the spruce budworm were recorded by Heimpel (1956). These have particular importance in determining the susceptibility of insects to certain pathogens.

Heron (1962) recently reported progress in the study of the role of chemical constituents of host foliage in determining feeding behavior. There is a chemosensory basis for the preferential feeding of budworm larvae with respect to young vegetative shoots, staminate flowers, and mature needles of white spruce. Relative sugar concentrations of the tissues is one factor, but other stimulants are involved. At least one constituent in mature needles has been shown to have a deterrent effect.

## LIFE HISTORY

The life history of the spruce budworm, as it occurs in the Central Rocky Mountain Region, was summarized by Wilford (1962a) as follows:

As second instar larvae, the budworm hibernates on the bark of the tree, from twig to bole, from late summer (August-September) to early spring (April-May) without having fed and without feeding.

A larva, upon emergence from its hibernaculum, moves to the foliage, will mine into an old needle, feed there for awhile, emerge, and attack a swelling bud, or it will go directly from its hibernaculum and bore into a swelling bud. Then the larva feeds on the developing needles within the bud and on the new needles growing from adjacent buds. As the needles develop, the growing (third to fifth instar) larva loosely binds the needles together with silk, forming a shelter. This shelter of silk, green needles, dead needles, bud scales, and frass protects the larva, and the larva spends most of its time within the shelter. When the supply of food within the shelter is consumed, the larva (fifth and sixth instar) moves out in search of more. After 3 to 4 weeks of feeding, the larva pupates,

generally within or attached to its shelter. The moth emerges within 10 days and mates. The gravid female lays masses of eggs, each mass on the undersides of a green needle, new or old.

The 2-year cycle budworm, a major variation from this generalized life history, has been described earlier. The 2-year cycle budworm is not known to occur in this region.

Prior to 1944, it had been accepted that young larvae always made their first attack on buds or young foliage. Atwood (1944), from his observations in western and northern Ontario, reported that the larvae "almost invariably" formed mines in old needles of spruce and balsam fir before attacking the buds. An unpublished report concerning an early budworm control project (Evenden 1932) contains an observation by B. H. Wilford that budworm larvae mined Douglas-fir needles prior to attacking the buds. McGugan (1954) found that most larvae mine only one needle before attacking the buds, but a few larvae may enter the buds directly and a few mine additional needles.

#### HEAD CAPSULE WIDTHS

Several workers have published tabulations of head capsule widths for the six instars. Regional differences occur, the western form being generally larger than the eastern form, especially in the last instar. Specifically, the sixth instar larvae of the 2-year cycle budworm (Shepherd 1953b) and the fifth and sixth instar larvae from Oregon (Bean and Batzer 1957) are larger than the same instars of eastern budworm. The measurement of head capsule widths is the best single criterion for determining the instars of larval populations.

## SEXING OF LARVAE

When the large silk (salivary) glands are stained by the Feulgen "squash" and temporary aceto-carminic smears (Smith 1943), certain deeply staining bodies appear in the resting nuclei of female budworm larvae (Smith 1945). These heteropycnotic bodies, restricted to the nuclei of females, are the sex chromosomes. (Heteropycnosis is defined as the tendency of the sex chromosomes to remain compact and stainable during the resting stage.) This technique is useful to determine the sex of first, second, and third instar larvae.

In fourth and later instar larvae, the male gonads are seen as darkly pigmented bodies (McGugan 1955). This characteristic is altered by the presence of certain parasites that inhibit the development of the testes, and male larvae cannot be distinguished from female larvae.

## POLYGyny

Campbell (1961) observed that, in captivity, the males of spruce budworm are capable of mating several times. It is pointed out that, on the basis of this observation, a shortage of males should not be considered a mortality factor in life table studies.

## GENETICS

Studies of the genetics of the budworm that lead to the determination of the specificity of C. pinus have been reported (Stehr 1959). Stehr also demonstrated that the occurrence of the brown female in populations of the eastern budworm is determined by a sex-linked and sex-limited gene (Stehr 1955).

Stehr reported that early work in crossing certain western and eastern spruce budworm populations resulted in an altered sex

ratio, a shortage of females (Stehr 1962). A possibility exists that artificial manipulation of the sex ratio could be used as a control technique.

Stehr (1953) also described a mutation that produced a few budworms with scarlet-red eyes that were larger than the normal dark purple plum-like colored eyes. The larvae with the mutation, up to the fifth instar, were pale and the testes unpigmented. A similar phenomenon has been observed in Ephestia kuehniella Z.

#### SPRUCE BUDWORM FECUNDITY

Campbell (1958) defined fecundity as the number of eggs laid by a female that has been successfully inseminated. He stated that the numerical value of fecundity is actually the quotient of egg weight and egg mass. He demonstrated that these two factors are determined by independent genetic systems. One system, acting during the larval period, determines the amount of body mass available for egg production. The other, acting during the pupal and adult stages, determines the weight of the eggs that are produced from that mass.

Extension of this study showed that the reproductive potential of a budworm population depends on the relative frequency of two types of X chromosomes (Campbell 1962a and 1962b). One determines small egg size, high fecundity, large body size, slow development rate, and low environmental resistance. The other determines large egg size, low fecundity, small body size, rapid development rate, and high environmental resistance. Campbell (1962a) suggested that the X chromosomes produce these characteristics by determining



different mitotic rates and consequently variations in the number and size of cells. This finding may be the key to the reasons for the numerical fluctuation of spruce budworm population levels.

Miller (1957) demonstrated the usefulness of regression equations based on pupal size and egg numbers. The technique is particularly useful in life table studies in which a value of fecundity is desired for a large number of plots and time is not available for oviposition trials on all the plots. The technique will also help detect moth invasion of a specific area. If the observed number of eggs greatly exceeds the expected values based on the regression equations, it is likely that an influx of moths from other areas has occurred. However, there is considerable error likely to occur if a regression equation is used for a population other than the one from which it was derived. This necessitates either constant checking of existing equations or the derivation of new ones.

The number of eggs per mass varies considerably from region to region. In eastern Canada, budworm egg masses average about 18 eggs (Morris 1954). Carolin and Coulter (1959b) base their damage predictions on the density of egg masses which generally contain about 45 eggs. Terrell (1961b) reported that there are usually about 40 eggs per mass in the Northern Rocky Mountain Region. In the central Rocky Mountains, there are usually 20 to 30 eggs per mass (Landgraf 1959; Wilford 1961, 1962a; Wilford and McKnight 1960) on Douglas-fir needles. On the wider and longer needles of white fir, the average number of eggs per mass approaches the number found in other areas.

Blais (1953) reported that budworm fecundity is reduced when the larvae are forced to feed on old foliage after the supply of current growth has been exhausted. Thomson (1958a) found that budworm fecundity was reduced by infection by Perezia fumiferanae.

The effects of food and disease on fecundity are discussed more fully in later sections of this review.

#### REARING TECHNIQUES

Stehr (1954) developed a method of rearing the spruce budworm in large numbers that appears to be commonly used in Canadian laboratories. The development of an artificial medium as a substitute for natural food would greatly advance the rearing techniques so necessary for nonfield studies.

Harvey (1954) demonstrated that nondiapause stock could be developed for laboratory cultures. Mortality, mating success, and fecundity were comparable to normal rearings. The percentage of non-diapausing larvae was 20.6 percent in the first generation and 38.5 percent in the second, but values as high as 80 percent were obtained. The length of a generation was 2 months for nondiapause stock and 6 months for normal rearings.

Wellington (Wellington, E.F. 1949a, 1949b) described an artificial medium that worked satisfactorily for rearing spruce budworm larvae. The medium consisted of 100 parts balsam fir suspension, 50 parts of 8-percent agar, 1.5 parts of 10-percent "Mycoban", and 1.5 grams of autolysed yeast. The suspension was prepared by placing the foliage in a blender and mixing it with a minimal amount of distilled water to

make a fine suspension. The "Mycoban", sodium proprionate, inhibited fungal growth but did not counteract material attractants, nor did it affect the growth or fecundity of the insects.

Dioryctria reniculella Grt. and Archips rosaceana Harr.

were also reared on the balsam fir mixture and Archips fervidana Clem. on a medium of red oak (Quercus rubra Duroi).

### ECOLOGY

#### A CONCEPT OF "ENVIRONMENT"

Andrewartha and Birch (1954) pointed out that for a given species each individual in a population will have its own developmental rate, longevity, and fecundity. For a given population, there will be a mean developmental rate, a mean longevity, and a mean fecundity. These mean values are determined, in part, by the environment and partly by a quality of the animal which Andrewartha and Birch term the "innate capacity for increase".

Andrewartha and Birch consider that environment applies to individuals, not to populations. Therefore, the environment of an individual includes animals of its own kind and animals of other kinds. They believe that any environment can be analyzed as four general sets of components--weather, food, other animals, and a place in which to live.

A great portion of the literature concerning the spruce budworm pertains to one or more of these components. The references reviewed in the sections to follow are organized in that manner.



## ENVIRONMENT-WEATHER

### The Temperature of Budworm Habitats

Wellington (1950a) reviewed the subject of the effects of radiation on the temperatures of insect habitats and made significant measurements and observations. He concluded that the differences he observed between insect temperatures or the temperature of their feeding sites on their food plants and the temperature of the surrounding air were large enough to be given consideration in field studies.

These differences are due to radiant heating in the day and radiant cooling at night. Spruce budworm larvae, in their webbed feeding tunnels, may be exposed to temperatures up to 8° C. above air temperature. The staminate flowers of white spruce are 5° to 8° above the temperature of vegetative buds in sunlight and may be 10° to 14° above air temperature.

#### Internal Temperatures of the Spruce Budworm

Shepherd (1958) demonstrated, in laboratory studies, a direct relationship between the readiation intensity striking a larva and the excess of larval temperature over air temperature. He found that in bright sunshine larvae on overstoried spruce reproduction had an average temperature excess of 2.3° C. and larvae on reproduction in a stand opening had an average excess of 3.7° C. Wind and evaporation reduced the temperature excesses.

#### Temperature Preference

Wellington (1949a) found that the budworm had no temperature preference as such. When he tested budworm larvae in graded

temperatures and rates of evaporation, he found that, below an upper limit of temperature, the larvae aggregated within specific ranges of evaporation regardless of where these ranges were placed within the temperature range. The upper limits of temperature beyond which the larvae did not travel when they were allowed to move freely in combined gradients of temperature and evaporation were as follows: For first instar larvae, about 28° C.; for instars two and three, about 36° C.; for instars four, five, and six, from 37° to 38° C. Below these upper limits, the larvae were indifferent to temperatures down to and including 10° C., the lowest temperature tested.

#### Threshold of Development

A temperature of 42° F. was used as a threshold of development by Mathers (1935), Henson (1948), and Wagg (1958) in their investigations. They appear to have assumed this to be the threshold of development and did not determine it experimentally.

#### Effect of Temperatures on Hibernating Larvae

An unseasonal cold wave in Montana that lasted 7 days in November 1959, and in which temperatures of -45° and -53° F. were recorded, appeared to have little effect on hibernating budworm larvae (Terrell 1960).

In Ontario, the emergence of second instar larvae from hibernation was shown to be closely related to April and May temperatures (Rose and Blais 1954). Abundant emergence was observed after spring temperatures had risen to 60° F., but temperature variations had corresponding effects on emergence. If the temperature rose suddenly to 60° F. from preceding low temperatures, emergence was delayed. If the rise was gradual, emergence followed almost immediately.

Laboratory studies by Bean (1961b) indicated that 2.5° C. approximated the threshold temperature that initiates diapause termination of hibernating larvae. By using this temperature as a base and calculating degree hours from thermograph records, it was possible to predict the approximate date of larval emergence in the field.

#### Effect of Temperatures on Feeding Larvae

In 1956, spruce budworm development in the Lower St. Lawrence and Gaspé regions was greatly retarded by temperatures cooler than normal in May, June, July, and August (Blais 1956 and 1958b). A shortage of current growth forced the larvae to feed on old foliage, retarding their development even further. At higher elevations development was retarded to the point that some pupae and many eggs did not emerge before cold weather in the fall. In November, sampling found 13 percent of the pupae still unemerged. Egg mass populations were high, but 53 percent were unhatched, 10 percent partially hatched, and 37 percent hatched. The eggs averaged only 11 per mass for 100 masses in contrast to the usual 20 per mass for this area.

Prebble (1945) reported a general reduction in the level of spruce budworm populations on three districts in Ontario because of late spring frosts that killed new shoots on balsam fir and white spruce trees when the growth was well advanced and the budworms were feeding. He observed that the frosts were responsible for killing many larvae due to direct freezing of the larvae and through the

destruction of the favored food. Also, insect parasites were very effective against the larvae that survived the damage by frost.

Similar budworm mortality by late freezes was reported in Colorado at Estes Park in 1945 (Dowden and Buchanan 1945) and on the Uncompahgre National Forest in 1947 (Buchanan 1948).

#### Effects of Evaporation Rates

Wellington has shown that spruce budworm larvae showed preferences for specific evaporation rates regardless of where these rates occurred in a range of temperatures (Wellington 1949a). The larvae always congregated in the one preferred zone of evaporation rate irrespective of temperature (Wellington 1949b).

The behavioral responses of the budworm larvae to different evaporation rates have great survival value as was pointed out by Wellington (1950b). First instar larvae spin their hibernacula in their preferred zone. The turning reaction of second instar larvae keeps them away from situations of excessive moisture. The rate of evaporation inside the feeding tunnels of sixth instar larvae is nearly identical to that of their preferred zone. When the tunnels are partially destroyed or consumed by feeding, the larvae move to a more favorable area. When the tunnels are flooded by rains and low rates of evaporation exist, the larvae react by dropping.

Shepherd (1959) studied the phytosociological and environmental characteristics of outbreak and nonoutbreak areas of the 2-year-cycle budworm. He concluded that the high mortality keeping populations at a low level is partially attributable, directly or indirectly, to the high moisture conditions or low evaporation rates. The evaporation

rates are determined not only by the weather systems but also by the habitats of the stands. The difference in evaporation rates between Peltigera and Tiarella associations increases with any regional increase in evaporation; this results in a comparatively greater "release" of the budworm in the Peltigera association.

#### Effect of Constant Temperature and Varied

##### Humidity on Pupal Development

Cook (1953), using the 2-year-cycle budworm, tested the effect of varied humidities while maintaining a constant temperature of 22° C. The humidities tested were 96, 83, 73, 67, and 39-percent relative humidity. The field conditions, for comparison, averaged 50 percent. The period for pupal development differed very little between the tested humidities, averaging 9.6 days for males and 8.8 days for females. The male pupae required 20.2 days for development, females 18.2 days, under field conditions. However, the cumulative degrees temperature above 43° F. (taken as a threshold of development) were nearly equivalent between the experimental and field conditions. In the experimental apparatus, 6,589 total degrees were required for the development of the male pupae, 6,040 for the female pupae. Under field conditions, 6,429 and 5,950 total degrees were required for male and female pupae, respectively.

Mortality was greatest at 30-percent relative humidity, lower and nearly equal at the other tested humidities. Mortality was much lower at field conditions. Mortality at 96 and 83 percent was due to mold, and at 73, 67, 39 percent and in the field, due to dessication.



## LIGHT REACTIONS OF SPRUCE BUDWORM LARVAE

Wellington (1948) reported that budworm larvae of all stages were at first positive to discrete light sources. First and second instar larvae retained this reaction under all conditions, starved third instar larvae were indifferent to light, and larvae of the last three instars, when starved, first performed light-compass reactions and then became photonegative. The larvae were photopositive when the digestive tract was distended and exhibited light-compass reactions or became photonegative when the digestive tract began to empty. All the larval stages were photopositive to diffuse light.

Wellington et al. (1951) reported further that the basic light reactions of the budworm larvae are related to their internal temperature. They react positively when cool but negatively when too hot. This was demonstrated in the field and in the laboratory and to both discrete and diffuse sources of light.

## LIGHT REACTIONS OF SPRUCE BUDWORM MOTHS

Wellington (1948) found that adult budworm males were photopositive. Nonflying females were photonegative, and flying females performed light-compass orientations.

Edwards (1962) found considerably less activity in female moths than in male moths. The flying activity of both sexes began in late afternoon or several hours before sunset on a clear day. Males had two periods of peak activity, one immediately after sunset and another about midnight. They were not active after sunrise. There was a period of peak activity for females just prior to sunset.

## EFFECT OF WIND ON SPRUCE BUDWORM LARVAE

Shepherd (1956) observed that a period of unusually strong wind reduced the number of fifth and sixth instar larvae on small Engelmann spruce and alpine fir trees from 4 or 5 to 1 per 5-foot tree. An 81-percent loss was recorded from artificially infested trees.

### SUMMARY OF THE EFFECTS OF PHYSICAL FACTORS ON THE BEHAVIOR OF THE SPRUCE BUDWORM

The observations of Wellington and Henson (1947) summarize the effects of physical factors on the behavior of the spruce budworm. The first instar larvae, on emerging from the egg, react positively to light and move to the tip of the needle on which the eggs were laid. Crowding may cause many to drop on their silken threads. The larvae that fall may drop to a twig below or they may be caught in vertical air currents and be carried above the trees. The larvae that drop to twigs below will again move to the periphery of the tree. Either event leads to dispersal.

If the larvae are shielded from the sun, they remain photopositive until they contact debris. Then a tactile response stimulates hibernacula construction. If the sky is clear and the larva becomes heated above the reversal temperature, it becomes temporarily photonegative and returns to the shade. If a larva emerges on an overcast day, it may spin its hibernacula where it could be dessicated by later hot, dry weather.

Emerging second instar larvae are strongly photopositive and are attracted to the periphery of the tree, the area of most suitable food. Again dispersal occurs by the same mechanisms as in the

previous fall. The larvae do not feed at temperatures less than 50° F., but direct sunlight may warm the foliage above air temperature and permit feeding. Since larvae feed in needles and buds at high humidities, some factor must counteract observed effects of low evaporation seen in later instars. Photic reversal, caused by starvation or high body temperature (100° F. in the sixth instar), produces dropping to lower levels. High temperature also causes movement to the interior of the tree. Vibration or flooding also causes dropping.

Adult females do not fly until they deposit 1 to 2 egg masses. Both sexes are subject to considerable dispersal. Males are photopositive when dark-adapted, but quickly become adapted to any light intensity and become extremely sluggish. Dark-adapted females exhibit photonegative or compassing behavior. Light-adapted females are also sluggish. Neither sex is active until twilight.

#### THE THEORY OF CLIMATIC RELEASE

A series of papers by Canadian workers proposed (Wellington et al., 1950) and later supported (Wellington 1952; Greenbank 1956; Pilon and Blais 1961) a theory of climatic release as a cause of spruce budworm outbreaks in Canada. The physical conditions ideal for budworm development are plenty of sunlight and lack of rainfall. The dry conditions that provide more sunlight in the spring and summer and continued cold in winter are more closely associated with polar continental air masses than with maritime air masses. Wellington et al. (1950) made a survey of known outbreaks in northeastern North America and found a recurrence of several biological



and physical phenomena in 3- or 4-year periods preceding known outbreaks. The annual numbers of cyclonic centers passing through a given area may be taken as indices of air mass movements. The numbers decreased before outbreak dates, so that outbreaks occurred during periods of decreasing or minimal numbers.

Official precipitation records are rough indices of both moisture and available sunlight. Precipitation fell below normal during the preoutbreak periods.

In areas of Ontario in mixed stands of poplar and balsam fir, heavy feeding by the forest tent caterpillar preceded spruce budworm outbreaks, and there were indications that a similar association might occur in western Quebec and in New Brunswick. Wellington concluded that forest composition is a preparatory cause of outbreaks but that relaxation of climatic control is the immediate cause of rapid population growth to the outbreak stage in susceptible foci.

Analysis of weather records supported this theory for outbreaks in Ontario (Wellington 1952), in New Brunswick for outbreaks which began in 1912 and 1949 (Greenbank 1956) and in Quebec for outbreaks between 1939 and 1951 (Pilon and Blais 1961).

#### ENVIRONMENT-PARASITES

A large complex of primary parasites is associated with the spruce budworm. The species which comprise the complex differ in space and time. The following authors have reported comprehensive studies of the parasites in specific outbreaks: Wilkes et al. (1948) in British Columbia; Dowden et al. (1948) in New York and Colorado; Dowden and Carolin (1950) in New York; Jaynes and Drooz (1952) in New York and

Maine; McGugan and Blais (1959) in Ontario; Carolin and Coulter (1959a) in Oregon; and Blais (1960) in Quebec.

In general, although parasitism is always an important mortality factor, the effectiveness of parasites is greatest only after another agent such as weather or starvation has considerably reduced the host population. The presence and relative abundance of alternate hosts greatly influence the nonspecific primary budworm parasites. Carolin and Coulter (1959a) believe that hyperparasitism may be responsible for reducing the effectiveness of primary parasites in the early stages of an outbreak.

### Dipteran Parasites

#### Biology

The biologies of some of the most important Dipteran parasites of the budworm are summarized in table 1. Our knowledge of these species is much more complete than for the Hymenopteran species. This has resulted from the intensive studies of the budworm parasites in a British Columbia infestation by Coppel and his associates. Keys to the puparia (Ross 1952) and to the adults (Coppel 1960) of the Dipterous parasites are available.

#### Seasonal Activity

In British Columbia, the adults of Madremyia saundersii emerge from their budworm hosts in early July (Coppel and Maw 1954b). There are two or three generations per year, one complete in the budworm. Sarcophaga aldrichi adults are active in the field from May to July in British Columbia (Arthur and Coppel 1953). Adults of Phryxe pecosensis are seen from May to October (Maw and Coppel 1953).

Table 1.--Summary of the life histories of the most important Dipteran species of spruce budworm parasites

| Species  | Stage :<br>: attacked                                   | Emerged from :<br>: budworm | Pupation :<br>: site     | Overwintering :<br>: habits             | Alternate :<br>: hosts                       | Reference   |
|--|---|-----------------------------|--------------------------|---|--|---|
| <u>Sarcophaga</u><br><u>aldrichi</u><br>Park.    | Prepupae or<br>pupae. (Eggs<br>or larvae<br>deposited.) | Pupae                       | Ground?                  | Puparium?                               | <u>Malacosoma</u><br><u>disstria</u><br>Hbn. | Arthur & Coppel<br>(1953)   |
| <u>Phryxe</u><br><u>pecosensis</u><br>(Tns.)     | Larvae<br>Large larvae                                  | Larvae or<br>pupae          | Ground?                  | Unknown<br>"In some other<br>host"      | Unknown                                      | Maw & Coppel<br>(1953)<br>Dowden & Carolin<br>(1950)                      |
| <u>Madremyia</u><br><u>saundersii</u><br>(Will.) | Larvae<br>Larvae (VI)                                   | Larvae (VI)<br>or pupae     | Ground                   | As first or<br>second in-<br>star larva | Unknown                                      | Coppel & Maw<br>(1954b)<br>Carolin & Coulter<br>(1959a)                   |
| <u>Omotoma</u><br><u>fumiferanae</u><br>(Tot.)   | Larvae <sup>2/</sup>                                    | Pupae                       | Ground                   | Puparia<br>Puparia                      | Unknown                                      | Coppel & Smith<br>(1957)<br>Coppel (1946)<br>Carolin & Coulter<br>(1959a) |
| <u>Phorocera</u><br><u>incrassata</u><br>Smith   | Larvae <sup>1,2/</sup>                                  | Pupae                       | In host<br>pupal<br>case | Unknown                                 | Unknown                                      | Coppel (1958)   |
| <u>Ceromasia</u><br><u>aureicaudata</u><br>Tns.  | Larvae <sup>1,2/</sup>                                  | Pupae                       | Ground                   | As larvae<br>in pupae<br>of alt.        | Fall webworm                                 | Coppel & Maw<br>(1954a)   |

1/ Eggs are deposited on leaves and later ingested.2/ Parasite does not develop until host pupates.3/ Eggs deposited on or near host.

Table 1 - continued

| Species                                   | : Stage :<br>: attacked :             | : Emerged from :<br>: budworm :          | : Pupation :<br>: site : | : Overwintering :<br>: habits : | : Alternate :<br>: hosts : | Reference   |
|---|---------------------------------------|--|--------------------------|---------------------------------|----------------------------|---|
| <u>Agria</u><br><u>affinis</u><br>(Fall.) | Late larvae<br>or pupae <sup>3/</sup> | Larvae,<br>prepupae but<br>usually pupae | Ground                   | Puparium                        |                            | Coppel et al.<br>(1959)   |
| <u>Aplomya</u><br><u>caesar</u>           | Large<br>larvae                       | Larvae or<br>pupae                       |                          | "In some<br>other host"         |                            | Dowden & Carolin<br>(1950)  |
| <u>Lypha</u><br><u>setifacies</u>         | Larvae                                |  | Ground                   | Puparia                         |                            | Wilkes, et al.<br>(1948)<br>Coppel (1946)<br>Carolin and<br>Coulter (1959a) |

3/ Eggs deposited on or near host.

Agria affinis adults, emerging from overwintered puparia, are active from mid-June to mid-July (Coppel et al. 1959). Ceromasia auricaudata adults are seen in the field in early June (Coppel and Maw 1954a).

Phorocera incrassata adults are seen throughout June and their progeny in July and early August. About 25 percent of the puparia of Omotoma fumiferanae produce adults the same year, the rest emerging the following year (Coppel and Smith 1957). Adults from overwintered puparia are active from May through June and into July.

#### Superparasitism

Phorocera incrassata.--Common but no more than one puparium is found in a host (Coppel 1958). Omotoma fumiferanae.--Common but no more than two parasites survive per host (Coppel and Smith 1957).

Agria affinis.--Never more than one larvae completes development in a host (Coppel et al. 1959).

#### Multiparasitism

Madremyia saundersii may parasitize budworm larvae already parasitized by Phytodietus fumiferanae, the former surviving at the expense of Phytodietus (Coppel and Maw 1954b). As many as three Phryxe peccosensis or combinations of Phryxe pecosensis and Aplomya caesar, but not more than two Aplomya may emerge from the same budworm host (Dowden and Carolin 1950). Multiparasitism by Omotoma fumiferanae with Phytodietus fumiferanae was observed, the one farthest developed surviving (Coppel and Smith 1957). Coppel (1958) did not observe multiparasitism involving Phorocera incrassata.



## Hyperparasitism

Omotoma fumiferanae was parasitized by Nasonia vitripennis (Coppel and Smith 1957). Hyperparasitism of Phorocera incrassata was not observed by Coppel (1958). Madremyia saundersii is killed by Amblymerus verditer (Coppel and Maw 1954b). Hyperparasitism of Agria affinis was rare (Coppel et al. 1959).

### The Role of Agria affinis

Agria affinis has been recorded as a parasite, predator (Coppel et al. 1959), and as a scavenger (Dowden and Carolin 1950). Dodge (1961b) believes that Agria affinis, Sarcophaga aldrichi, and S. hinei will oviposit only on fresh host material and are not able to withstand the competition of more aggressive filth-breeding species.

## Hymenopteran Parasites

### Biology

Some of the known features of the biologies of some of the Hymenopteran parasites of the spruce budworm are summarized in table 2.

### Superparasitism, multiparasitism, and hyperparasitism

Low incidence of superparasitism by Apanteles fumiferanae suggested to Miller that the species can discriminate between parasitized and nonparasitized hosts (Miller 1959).

In two seasons' study in British Columbia, Coppel found the effects of superparasitism on Phytodietus fumiferanae to be negligible, its effectiveness was reduced at least 3 percent by multiparasitism and 17.9 percent by hyperparasitism (Coppel 1953).

Table 2.--Summary of the life histories of the most important Hymenopteran species of spruce budworm parasites

| Species   | : Stage :<br>: attacked : | : Emerged from :<br>: budworm :     | : Pupation :<br>: site : | : Overwintering :<br>: habits :        | : Alternate :<br>: host : | References                                      |
|---|---------------------------|-------------------------------------|--------------------------|--|---------------------------|---|
| <u>Apanteles</u><br><u>fumiferanae</u><br>Viereck | Instar I<br>and II        | Instar IV or V                      | Cocoon on<br>foliage     | Eggs or larvae<br>in host              |                           | Brown (1946a), Miller<br>(1959)                 |
| <u>Glypta</u><br><u>fumiferanae</u><br>(Viereck)  | Instar I<br>and II        | Instars V<br>and VI                 | Cocoon on<br>foliage     | Eggs or larvae<br>in host              |                           | Brown (1946b), Miller<br>(1960)                 |
| <u>Phytodietus</u><br><u>fumiferanae</u><br>Rohw. | Late instar<br>larvae     | (Feeds extern-<br>ally)             | Cocoon on<br>foliage     | In cocoon as<br>mature larva           |                           | Coppel (1946), Wilkes<br>et al. (1948)          |
| <u>Horogenes</u><br><u>cacoeciae</u>              | Instar I<br>and II (?)    | Larva (V)                           |                          | In host larvae                         |                           | Coppel (1946), Carolin<br>& Coulter (1959a)     |
| <u>Phaeogenes</u><br><u>hariosolus</u>            | Pupae                     | Pupae                               |                          | As adult                               |                           | Coppel (1946)<br>Carolin and Coulter<br>(1959a) |
| <u>Apechthis</u><br><u>ontario</u>                | Pupae                     | Pupae                               |                          | Mature larvae<br>in host pupal<br>case |                           | Coppel (1946)<br>Carolin and Coulter<br>(1959a) |
| <u>Meteorus</u><br><u>trachynotus</u><br>Vier.    | Larvae                    | Late instar<br>larvae <sup>1/</sup> |                          | In alternate<br>host                   | Unknown                   | Dowden & Carolin (1950)                         |
| <u>Trichogramma</u><br><u>minutum</u><br>Riley    | Eggs                      | Eggs                                | Egg                      | Unknown                                |                           | Carolin and Coulter<br>(1959a)                  |

<sup>1/</sup> Prevents host larvae from pupating.



Nasonia tortricis and Amblymerus verditer attack Itoplectis conquisitor and Ephialtes ontario, but may also be primary parasites (Dowden and Carolin 1950).

Itoplectis obesus, Ephialtes ontario, Scambus hispae, and Amblymerus verditer were recorded as primary parasites of the budworm and also were reared from cocoons of Phytodietus fumiferanae (Coppel 1946).

Hyperparasitism was not uncommon in Ontario but does not appear to be a limiting factor for any parasite species (McGugan and Blais 1959).

Multiparasitism studies by Lewis showed that only one parasite of either species, Apanteles or Glypta, could survive in a single host (Lewis 1960). He observed inhibition effects on Glypta eggs by Apanteles larvae. This effect became more pronounced as the time span between oviposition of the two parasites was increased.

#### The Egg Parasite, Trichogramma minutum Riley

This species seems to be the only parasite of spruce budworm eggs. It generally does not cause a high mortality, but Miller (1953) recorded parasitism as high as 48 percent in 1950 at Green River. Miller suggested two factors that appear to limit the effectiveness of Trichogramma. This species requires the presence of hosts other than the budworm prior to budworm oviposition. The abundance of alternate hosts will influence the number of budworm egg parasites. Also, the number of eggs deposited in each host egg (an average of 3.7 adult parasites emerged from each parasitized host egg in 1950)

limits the total number of host eggs that can be parasitized. This factor reflects characteristics of poor searching ability and high oviposition rate.

Miller (1953) found the percentage of budworm eggs parasitized to be greater in the top half of the tree crown. This was attributed to the relative amount of light. The plot on which this was observed was a dense young stand with the lower crowns partially shaded.

#### Factors Affecting Assessment of Parasitism by Apanteles and Glypta

It has been a common practice to force hibernating second instar spruce budworm larvae from their hibernacula and dissect the emerging larvae to detect the presence of these two parasites. Several factors have been found to affect samples obtained for this purpose and, unless they are taken into account, biased estimates of parasitization are obtained.

Jaynes (1954) removed branches from different heights on balsam fir trees in a medium infestation in Maine. All larvae that emerged from the branches were dissected. When the data were grouped by height of branch in feet from the ground, the percent parasitization by both Apanteles and Glypta increased with increasing height. When the data were grouped by portion of the crown from which the branches were removed, the percentages parasitization by Apanteles were 14 percent, 21 percent, and 35 percent for the lower, middle, and upper thirds, respectively. Percentages parasitization by Glypta were 6 percent, 10 percent, and 9 percent, respectively.

A second series of trees was sampled at the three crown levels, and the parasitization by Apanteles was 15 percent, 20 percent, and 27 percent for the lower, middle, and upper crown thirds. The means were significantly different (at the 5-percent level). It was concluded that parasitization at midcrown is a reliable indication of the average parasitization for the whole tree.

Dodge (1961a) conducted a similar study on infested trees, mostly Douglas-fir, in Montana. He found that parasitism by Glypta was significantly greater in the middle and upper crowns than in the lower crown. Combined parasitism was greatest in the midcrown, and limbs from this portion of the crown would give an exaggerated estimate of parasitism. He showed further that Glypta is more common in budworm larvae hibernating under bark scales and that Apanteles was most common in larvae hibernating in the foliage. He concluded that a limb from the lowest whorl of vigorous branches would probably give the best indication of parasitism for the tree.

Lewis (1960) reported other factors affecting assessment of parasitism by these two species. He found Apanteles to be more efficient in attacking mobile budworm larvae and Glypta more efficient in attacking larvae in their hibernacula. He also found that nonparasitized second instar larvae are strongly photopositive, while parasitized larvae are photonegative, or do not react at all to light. In addition, parasitized larvae emerge from their hibernacula as much as 7 to 10 days later than nonparasitized larvae. These factors could greatly bias the estimates of parasitism

obtained by dissecting larvae that have been induced to collect in lighted vials placed in tight containers.

Lewis and other workers have observed increases in percent parasitism when measured when the budworms were in the bud-mining stage as compared to estimates based on dissections of overwintering larvae. He explains this as differential loss of parasitized and nonparasitized larvae. The less active behavior of parasitized larvae makes them less susceptible to dispersal loss, and since they leave their hibernacula later, the favored buds are more likely to be available for food.

Lewis also found no significant difference in percent parasitism on a 15-inch twig compared to the rest of the branch at either collection time.

Bean (1962) analyzed data on parasitism of budworm pupae in northeastern Minnesota to determine if parasitism by four major pupal parasites differed among crown classes and among crown levels. He found that a random sample of crown classes would be satisfactory, but that all crown levels should be sampled to give reliable estimates of pupal parasitism.

#### The Effect of Control Operations

##### on Apanteles and Glypta

Coulter (1954) reported that the parasites that attack hibernating budworm larvae would survive the aerial applications of DDT for budworm control in Oregon and Washington. Macdonald (1959) reported higher proportionate survival of Apanteles compared to Glypta in areas of New Brunswick sprayed with DDT from 1952 to 1958. He



gave three reasons for this: (1) Apanteles emerge from the host earlier than Glypta and spin cocoons and are relatively safe from poisoning; (2) parasitized hosts are less likely to contact residual insecticide than are healthy, active larvae; and (3) well developed Apanteles larvae appear able to emerge from "knocked down" hosts; Glypta was not observed to do this.

#### Interpretation of Mortality Data

It is generally agreed that a percentage mortality as such is not adequate to appraise the effect of controlling agents, particularly parasites, of insect populations. Variation is an important characteristic of mortality, and it is of great importance to follow the effect of a given mortality factor through several generations to determine the extent and direction of the variation (Thomson 1928; Morris 1957). Morris (1957) stated that low but variable mortalities might have a greater effect on population trend than greater but more constant mortalities. Variation in individual mortalities should be interpreted according to their effects on population trend rather than on generation mortality only.

To estimate the degree of parasitism in a population, samples are obtained from the host population and treated in such a way as to determine the abundance of parasites in the sample. This abundance is usually expressed as a percentage of the host individuals in the sample killed by the parasite species. Thomson (1928) termed these percentages as "apparent" mortalities and distinguished them from "real" mortalities. "Real" mortalities, Thomson believed, should be based on the initial or egg populations. Thus, with the

exception of observations of the mortality caused by egg parasites, entomologists usually measure apparent rather than real mortalities. Bess (1945), on the other hand, while he retained Thomson's interpretation of apparent mortality, believed that real mortalities should be based on the survival or adult population.

Miller (1955) used apparent parasitism and population trend during the larval stage as the basic data to assess budworm larval mortality due to parasites. Apparent parasitism was estimated from samples of the host population. The life history of the parasite was divided into a "pre-emergence" period, when the parasite is developing at the expense of the host, and an "emergence" period, when the host is actually killed. The real mortality is based on the host density at the beginning of the emergence period.

Thomson (1928) recognized two classes of mortality factors: "general or independent" factors whose action is independent of host density, and "individualized or dependent" factors whose destructive capacity depends in some way on host density. Parasites belong to the second class. Bess (1945) based his interpretations on these assumptions: (1) that all mortality factors are independent and not related to host density, and (2) that parasites attack their hosts indiscriminately, whether they are already diseased or contain another parasite or not. Andrewartha and Birch (1954) do not recognize "density-independent" factors and discount the importance of "density-dependent" factors.



Efforts to Increase Biological Control  
of the Budworm

Heimbürger (1945) discussed the proposal to control the spruce budworm in New Brunswick and Maine by an artificial change in species composition, "preferably by almost completely eliminating balsam fir". He expressed his convictions that this approach would not succeed. He discussed other approaches, chiefly population genetics of the budworm and its parasites and the interaction with balsam fir and other hosts. He considered the budworm biologically "young" in relation to its environment with high requirements for population pressure sufficient to cause outbreaks and low control by its parasites. He believed the budworms of other spruce and pine species in other regions "mature" and advocated the introduction of "mature" parasites of "mature" budworms for biological control.

Stairs and Bird (1960) described an occurrence of unusual parasitism of the budworm that points out the importance of "foreign" parasites. Second instar larvae were transferred from a natural infestation in Ontario to Sault Ste. Marie. They were placed on small balsam fir trees near an adjacent stand of sugar maple, white oak, white birch, balsam fir, and white spruce. The natural budworm populations at Sault Ste. Marie were very low.

Parasitism of the transferred larvae was high. Of the recovered larvae, 10 percent were killed by Apanteles and Glypta and 55 percent by Clinocentus sp. Clinocentus is normally a rare parasite of budworm and was not found in the original budworm population in Ontario.

Its natural host was probably Argyrotoxa semipurpurana Kft. which was epidemic on oak in the adjacent stand at Sault Ste. Marie.

Fye et al. (1962) recently reported progress in the search for alternate hosts of spruce budworm parasites in Ontario. Rearings of Lepidopterous defoliators from spruce, balsam fir, aspen, and white birch recovered many species of budworm parasites. Studies of this type will make contributions of considerable importance to the knowledge of the ecology of budworm parasites and are likely to lead to techniques to improve the effectiveness of biological control.

#### ENVIRONMENT-PREDATORS

##### The Role of Birds in Budworm Outbreaks

Predation by birds has been cited as a natural control factor in several spruce budworm outbreaks. Their effect on population trend is not clearly understood, but their effectiveness against high budworm populations appears limited.

George and Mitchell (1948) attempted to calculate the extent of budworm control exerted by insectivorous birds in an outbreak in New York. A systematic census in the Lake Clear outbreak area found the density of insectivorous birds to be three pairs per acre. The authors used two and one-half pairs per acre as the number of adult birds feeding chiefly or entirely on the budworm. These five birds and two nestlings per nest were present during the 40 days when the budworm larvae were most susceptible to predation. The authors estimated that the adults would consume about 1,200

grams of budworms and the young birds 750 grams, or a total of about 35,524 budworms. The budworm population was estimated at 500,000 to 1,000,000 per acre. Thus, the degree of control would be only 3.5 to 7 percent. These calculations do not take into account the number of eggs and first and second instar larvae consumed in late summer, fall, winter, and early spring. Kendeigh (1947) estimated 4.3 percent control in Canada, where the budworm population was estimated to be 376,000 per acre and the numbers of birds to be 3.19 pairs per acre. He referred to estimates of 13-percent control in 1918 in New Brunswick and 39 percent in British Columbia.

Predation by birds was studied as a natural control factor in a Maine outbreak from 1949 to 1951. On two study areas birds were undisturbed, and on a third an attempt was made to shoot all birds observed during the critical period of budworm development when they were most susceptible to predation. The percent reduction of budworms was 11 and 29 percent in 1949 and 1950, respectively, on the area where the birds were shot; 69, 56, and 56 percent in 1949, 1950, and 1951 on check area number 1, and 48 and 71 percent in 1950 and 1951, respectively, on check area number 2 (Dowden et al. 1953).

Analysis of stomach contents of 826 birds showed that 21 and 40 percent in 1949 and 1950, respectively, of the food consisted of budworms. Nearly all of the contents of stomachs from red squirrels collected in 1950 were insects, 51 percent were budworms (Dowden et al. 1953).

Mitchell (1952) presented a list of 45 species of birds from which the 826 stomachs were taken for analysis. Table 3 was taken from his data and presents the "feeding pressure" values of 14 of

Table 3.--Feeding pressure values of the most important insectivorous  
resident birds in a Maine spruce budworm outbreak (from  
Mitchell, 1952)

| Bird<br>species        | 1949-1950 average<br>feeding pressure |
|------------------------|---------------------------------------|
| Bay-breasted warbler   | 3.36                                  |
| Olive-backed thrush    | 2.36                                  |
| Magnolia warbler       | 2.02                                  |
| Purple finch           | 1.64                                  |
| Robin                  | 0.92                                  |
| Cape May Warbler       | 0.90                                  |
| Black burnian warbler  | 0.48                                  |
| Myrtle warbler         | 0.46                                  |
| White-throated sparrow | 0.33                                  |
| Slate-colored junco    | 0.26                                  |
| Solitary vireo         | 0.21                                  |
| Tennessee warbler      | --                                    |
| Nashville warbler      | --                                    |
| Red-breasted nut hatch | --                                    |

the most important resident species. For each species this value is obtained by multiplying its resident population (pairs per 100 acres) by the average volumetric content of sample stomachs and multiplying the product by the average percent budworm content.

The cedar waxwing was entirely a visitor, and no feeding pressure values could be calculated. The budworm occupied 89 and 84 percent of the volume of waxwing stomachs examined in 1949 and 1950.

It was concluded from these studies that birds were of little significance in an outbreak but may play an important role in maintaining endemic populations.

In the Green River outbreak, Morris et al. (1958) found that some birds presented a direct numerical response to budworm populations. Three of these species were the bay-breasted, blackburnian, and Tennessee warblers. Three other warblers showed an inverse response, probably due to competition from the three species showing a direct response. The predators were found to be of little control value during the outbreak.

#### Predation by Other Insects

Thomson (1957) examined 400 pupal sites on the Uxbridge Forest, Ontario, in 1956, 3 days before adult flight began. Ants were observed to be of considerable importance in addition to the insects listed in the tabulation below:



|   | : Number | : Percentage |
|---|----------|--------------|
| Whole pupae                               | 327      | 81.8         |
| Attacked by budworm<br>(VI instar larvae) | 10       | 2.5          |
| Attacked by Coleoptera                    | 9        | 2.2          |
| Attacked by <u>Dioryctria</u>             | 23       | 5.8          |
| Attacked by Syrphidae                     | 2        | 0.5          |
| Attacked by unknown                       | 29       | 7.2          |
| <hr/>                                     |          |              |
| Total attacked                            | 73       | 18.2         |

Earlier, Warren (1954) described the relationship between Dioryctria reniculella Grt., the spruce needle worm, and the spruce budworm. Under natural conditions, the two species compete, since both are defoliators of new growth. New foliage becomes scarce when defoliation is severe. A laboratory experiment indicated that predation of the budworm pupae by the needle worm greatly increased when only old foliage was supplied. No observations were made under field conditions to test this observation. Predation of budworm pupae in 1948 when the needle worm populations were highest may have caused the reduction of budworm populations observed in 1949.

Liscombe and Lejeune (1949) reported that "hordes of dragonflies were observed preying on budworm larvae in 1948...".

Predation by solitary wasps including Ancistrocerus catskill albophalteratus (Sauss.), A. tigris tigris (Sauss.), and Rygchium leucomelas (Sauss.) was studied by Fye (1962). The peak first



generation nesting activity of these species coincides with the late instars of the budworm and other spruce-fir defoliators. The wasps provision their nests with paralyzed defoliator larvae.

#### Predation by Spiders and Mites

Morris (1948) reported predation of budworm larvae and eggs by spiders.

Loughton and West (1962) described some interesting work in which they assessed spider and mite predation on the budworm. By serological techniques they were able to determine what percent of a given predator population had fed upon the budworm.

#### ENVIRONMENT-DISEASES

Bird and Whalen (1949) reported the presence of viruses, fungi, bacteria, and a protozoan in a survey of pathogens present in budworm populations of Ontario.

#### Virus Diseases of the Spruce Budworm

Bergold (1950) reported observations of electron micrographs of purified preparations of the viruses causing polyhedral diseases in C. fumiferana, Lymantria dispar, and Bombyx mori. He observed morphologically different forms which he described as stages of multiplication.

Quantitative infection tests found the budworm to be highly resistant or immune to the virus (Bergold 1951). It was not determined whether this was because of low virulence of the virus or because the insect was resistant or immune due to previous sublethal infections. Bergold felt the latter to be more probable. The fact that a certain percentage of orally infected budworms developed into adults indicated some degree of immunity.

Two features of the budworm life history have considerable influence on the transmission and dissemination of the virus. The feeding period of the budworm is relatively short, but the time of infection to death is rather long (10 days). Healthy larvae do not have much time to infect themselves by contact with dead individuals before pupation. It was not known if transovarial transmission of the virus occurred. If it did, the infected second instar larvae would die in their hibernacula and healthy larvae would not have an opportunity to come in contact with them.

Bird and Whalen (1954) reported that the budworm was susceptible to another virus. The first, described above, is characterized by the formation of polyhedra within the nuclei of tracheal matrix, fat, hypodermal, and blood cells. The second is characterized by the formation of polyhedra in the cytoplasm of mid-gut cells.

The infectious nature of the cytoplasmic polyhedra was described. Larvae fed the polyhedra developed the disease within 72 hours. Many larvae survived, indicating that the disease was not particularly virulent, or that infected mid-gut cells sloughed off and were replaced.

Krywienczyk et al. (1958) reported that the polyhedral and capsular viruses of the budworm belong to the two serologically distinct groups since no cross reaction occurs. This finding justified the previous distinction of the two groups based on differences in size and shape of the inclusion bodies, the morphology of the virus particles, and the developmental site of the inclusion bodies in the nucleus or cytoplasm. The capsular virus of C. fumiferana and C. muriana (the European counterpart of the spruce budworm) cross-reacted strongly, but there was no cross reaction between the polyhedral virus of C. fumiferana and either capsular virus.

Bird (1958) found that the cytoplasmic or granulosis virus that he and Whalen (Bird and Whalen 1954) had described earlier could also infect fat, hypodermal, tracheal matrix, and blood cells. The virus develops in the cytoplasm of these cells, whereas the polyhedral virus develops in the nucleus of these same cells. He found that prior infection of a cell by one virus interferes with infection by the other (Bird 1959; Bird and Stairs 1962). To produce double infections, an advantage must be given to the granulosis virus either in time or infectious units. Adjacent cells are frequently infected with different viruses, but usually blocks of cells are infected with the same virus.

Stairs and Bird (1962) reported field tests against the budworm using both the nuclear polyhedral virus and the granulosis virus. In both 1959 and 1960, all virus applications caused mortality, and no virus mortality was found on unsprayed trees. In 1960, the greatest mortality (61.5 percent) was on trees sprayed with granulosis virus, but mortality was more rapid on trees sprayed with the polyhedrosis virus. The authors pointed out that the practical use of the viruses depends on (1) development of efficient methods of virus propagation, (2) knowledge of most efficient concentrations to apply, (3) determination of the most susceptible stage of the insect, and (4) whether the viruses persist from year to year.

#### Fungi Associated with the Spruce Budworm

McLeod (1949) reported that a 1948 survey of fungi that parasitize, or grow in association with the spruce budworm, found

Hirsutella sp. to be most frequently isolated from diseased larvae.

Usually, there was no evidence of external mycelium. In 1947, however, diseased larvae had been coated with mycelium and had had numerous long, black, rigid hairs. The drier conditions of 1948 were considered responsible for the difference.

Hirsutella sp., Empusa sp., Beauvaria sp., and Isaria sp. were considered the most important genera found in fungus-infected budworm larvae (McLeod 1949).

#### The Microsporidian Disease of the Spruce Budworm

Thomson (1955) reported studies of the protozoan disease of the budworm reported earlier by Bird and Whalen (1949) and found the causal agent to be a new species of the order Microsporidia, and for it he proposed the name Perezia fumiferanae. In laboratory-reared insects, the principle site of infection is the cells of the mid-gut. The Malpighian tubules are frequently involved and occasionally small areas of muscle tissue. In naturally infected insects, the fat body, silk glands, epidermis, gonads, hind gut, and nerve tissue are also invaded. Thomson explained this difference by the fact that laboratory-reared insects receive a large number of spores and die quickly, whereas naturally infected insects receive small numbers of spores, live longer, and the parasite spreads throughout the body. He postulated that the mid-gut is probably where the parasite exerts its lethal effect. Only the cytoplasm of the host cells is invaded. The disease produces no apparent external symptoms, even for several hours after death.



Thomson (1958c) described the epidemiology of the parasite. There are two methods of infection, oral and congenital. All infected females transmit the parasite to their offspring, and for practical purposes all the progeny of such females are infected. Infected males are sometimes capable of transmitting the parasite to a portion of their offspring. Congenital transmission is responsible for the passage of the parasite from host generation to generation. Increase in the incidence of the parasite occurs by oral ingestion of spores, but the habits of host larvae restrict most transmission to the late larval instars.

Infection of the budworm by Perezia fumiferanae retards both larval and pupal development and reduces pupal weight, fecundity, and adult longevity, these effects being more pronounced in female insects (Thomson 1958a). Thomson found no evidence that the parasite affects male fertility, mate choice, or the fertility of the eggs produced. The parasite causes some mortality, most of which occurs before the fifth instar. Among larvae infected orally, mortality seems to be related to the size of the initial dose. The development and survival of the first instar and the overwintering second instar larvae are not affected. Thomson suggested that most of the observed results were caused by reducing the insects' ability to assimilate food. Mortality, however, was believed to be due to the destruction of the mid-gut or Malpighian tubules.

Neilson (1956) found the disease in spruce budworm adults collected at Green River in 1954 and 1955. As many as 42.6 percent of the collections were infected by microsporidia. Some adults

died soon after emergence from the pupal case. Some were so badly infected that they could not have mated or produced viable eggs or sperm. He pointed out that this may help to explain why, in some areas, fewer eggs are found than would be expected based on the number of empty female pupal cases.

It was observed that the disease caused by P. fumiferanae Thom. and either Apanteles or Glypta could occur in the same budworm host. Thomson (1958b) reported the results of a study made to determine the effects of the microsporidian on the Hymenopterous parasites. Prepared specimens of Apanteles and Glypta larvae from infected budworm larvae showed large numbers of spores confined only to the gut and they never invaded the tissues of the parasites. The parasite larva has a blind gut, and as spores are ingested they accumulate, being neither digested nor able to infect the parasite.

The parasite larvae emerging from the budworm were unable to complete development. Normally, the parasite larvae store food in their blind-sac mid-guts to last them through pupation. When the mid-gut is nearly filled with inert spores, not enough food can be stored, and the parasite dies of starvation.

#### Bacterial Diseases of the Spruce Budworm

Denton (1960b) reported that laboratory and field tests showed that Bacillus thuringiensis Berliner is toxic to spruce budworm larvae when a sufficient amount of the pathogen is ingested. The problem is to get adequate coverage of the pathogen over the foliage so that it will be consumed by the budworm larvae. Denton thought that dosages greater than those used with DDT would be necessary to achieve adequate control.



Mott et al. (1961) reported the results of some trials of aerial applications of Thuricide, a commercial formulation of B. thuringiensis. The insecticide did produce some budworm mortality but not sufficient to consider its use in place of DDT. Reports of spray formulation, toxicity, diagnosis, and bacteriological assay of spray deposit are included in the same issue of the Bi-monthly Progress Report.

Kushner and Harvey (1962) suggested that the antibacterial substances in the leaves that insects eat may play a direct part in protecting them against ingested bacteria but not against bacteria injected into the hemolymph. The authors present evidence that an increase in antibacterial activity of foliage eaten, an increase such as may occur with increasing age of foliage, can render an insect more resistant to bacterial attack. The increased sensitivity of a bacterial strain to inhibitory substances in leaves is accompanied by lowered pathogenicity.

Spruce budworm mortality was obtained by the injection of Bacillus cereus into the hemolymph but not when the same pathogen was fed to a similar group of insects on balsam fir foliage. Serratia marcescens was reported to have caused mortality in budworms reared in the laboratory on balsam fir. This pathogen was not inhibited, in plate tests, by balsam fir extract or the gut contents of budworms that had been fed on balsam fir foliage.

#### ENVIRONMENT-FOOD

The flowering of balsam fir has frequently been cited as one of the major factors in the epidemiology of the spruce budworm in northeastern North America.

### Flowering of Balsam Fir

Morris (1951) reported the effects of flowering on balsam fir trees at Green River, New Brunswick. Flower production begins 20 to 30 years after the initial release of the tree and increases directly with age, with respect to both the proportion of trees flowering and the intensity of flowering on individual trees. At Green River, heavy flower and seed production occurs every 2 years.

Depressions in the growth of primary branch terminals, leaders, and annual rings occur in flowering years. The quantity of new foliage produced by balsam fir in flowering years is much less than in nonflowering years. The sections of the crown that produce the most staminate flowers also produce the greatest weight of foliage in nonflowering years.

Flower buds appear on current growth near the end of the growing season and open the following spring. Female flowers are produced largely on the apical 5 feet and male flowers on the next 10 feet. Flower production in the lower crown depends on light intensity.

### Effect of Flowering of the Host

#### on the Spruce Budworm

The observations of Bess (1946) probably lead the way to more intensive studies by other workers. Bess observed that feeding was more extensive, larval development more rapid, and larvae more abundant on staminate balsam fir trees than on nonstaminate trees. He made similar observations in regard to black spruce.

Jaynes and Speers (1949) made similar observations in 1946 and 1947 in northern New York. Larvae feeding on balsam fir with

staminate flowers were slightly more developed than on balsam fir without such flowers. Moths from larvae fed on pollen showed no increase in fecundity, and no effect on the sex ratio was observed. In 1947, a year of abundant staminate flower production on balsam fir and spruce, a sharp reduction in the budworm population occurred.

Studies on spruce budworm populations on flowering and non-flowering trees were reported by Blais (1952). He found generally more eggs on the flowering trees. The flowering balsam fir trees were found to harbor higher populations in the early larval stages owing to the presence of staminate flowers and flower cups on these trees.

Larvae that fed partially on pollen developed more rapidly than larvae that fed exclusively on foliage. Pollen as a food did not appear to have any direct effect on survival or fecundity.

Defoliation was more severe on flowering trees in the earlier stages of the infestation. However, as populations increased, wandering increased because of competition for food. This resulted in an overflow of larvae from flowering to nonflowering trees.

Other experiments showed that mortality was higher, development retarded, and fecundity reduced in insects forced to feed on old foliage in contrast with those fed on current year's growth (Blais 1952). Blais found that when budworm populations destroy all current growth prior to completion of the larval stage, the number of eggs per surviving female decreases, and fecundity increases again when populations decline to where defoliation is not complete (Blais 1953). He also noted that gravid females reared on old

foliage or collected from an area of complete defoliation were able to fly before ovipositing. This is in contrast to other observations that fully gravid budworm female moths were not able to fly until they had deposited one or more egg masses.

Another effect of staminate flowers was observed by Wellington and mentioned earlier in this review. He observed (Wellington 1950a) that the staminate flowers of white spruce are 5° to 8° C. above the temperature of vegetative buds in sunlight and may be 10° to 14° above air temperature. This "greenhouse" effect would help to explain why larvae on trees bearing staminate flowers develop more rapidly.

Carolin (1950) conducted staminate flower studies at mid-crown on Douglas-fir trees in Oregon. Three pairs of trees were tested, each with one tree with staminate flowers and one without flowers. The final stage of larval development was reached at the same time on both types of trees.

Shepherd (1953a), in his studies of the 2-year-cycle budworm, reported on the variation in flowering of alpine fir. He stated that, "The flowering on the outbreak area was double that on the nonoutbreak area in the preoutbreak period." However, there was only a small amount of flowering at any time. Most trees produced no flowers, and then only the favorable branches in the upper crowns of a few large trees produced flowers. Even in good years less than 20 percent of these branches produced flowers. Thus, only a small percentage of the budworm population would be affected.



### Other Host Relationships

Blais (1957) reported that spruce budworm larvae feeding on black spruce had a slower rate of development and a higher rate of mortality than those feeding on white spruce or balsam fir. This was attributed to the lateness in opening of the black spruce buds rather than to the inferior nutritional quality of the foliage. When staminate flowers were present in abundance on black spruce trees, development and survival of the insect was fairly similar to that on the other two species. The flowers provided adequate food at the time of the third and fourth instars, thus permitting the larvae to survive until the opening of the shoot buds. The late opening of the black spruce buds explains the relative immunity of black spruce to severe spruce budworm damage.

Ghent (1958a) reported on his study of the relationship between the mortality of overstory trembling aspen to outbreaks of the forest tent caterpillar and the spruce budworm. Wellington et al. (1950) had pointed out that forest tent caterpillar outbreaks in aspen regularly preceded outbreaks of the spruce budworm in balsam fir. In a mixed stand, anything that hastens the succession from aspen to dominant conifers increases its susceptibility to spruce budworm outbreak. Temporary defoliation of the aspen has the same effect if the climatic conditions are ideal for a budworm outbreak.

Ghent found that the Lake Nipigon spruce budworm outbreak began in an area of decadent aspen stands, the remnants of which had been defoliated by the forest tent caterpillar just before the budworm outbreak. The initiation of the spruce budworm population



upsurge corresponded exactly with the period of heavy aspen defoliation. Flowering of balsam fir increased with aspen mortality. Ghent did not support the suggestion (Wellington et al. 1950) that the forest tent caterpillar defoliation accelerated overstory elimination and that the succession of coniferous component was hastened by this. He did not contradict the suggestion that the forest tent caterpillar defoliation extended the area of balsam fir and spruce susceptible to the budworm, but he did not consider the defoliation necessary.

#### The Chemosensory Basis for Preferential Feeding Behavior

Heron (1962) recently reported on laboratory studies of the role of chemical constituents of host foliage in the feeding behavior of the spruce budworm. These studies have established that there is a chemosensory basis for the preferential feeding behavior of budworm larvae with respect to developing vegetative shoots, staminate flowers, and mature needles of white spruce. This is determined in part by the relative sugar concentrations of the tissues, but other feeding stimulants are also involved. At least one constituent in mature white spruce needles has been shown to have a deterrent effect.

### ENVIRONMENT-ASSOCIATED INSECTS

#### Other Lepidoptera

Buchanan (1947) noted the presence of Dioryctria reniculella in association with the spruce budworm at La Veta, Colorado, in 1946.

Miller (1950) presented a key to some Lepidopterous larvae associated with the spruce budworm at Green River, New Brunswick.

The species keyed were Acleris variana, Recurvaria sp., Dioryctria reniculella, Zeiraphera fortunata, Archips persicana, Tortrix packardiana, Z. ratzeburgiana, Eucordylea strupictella and Griselda radicana.

The relationships, other than parasitism and predation, of other insects to populations of the spruce budworm do not appear to have been studied.

#### The Relationship of the Spruce Budworm to Subsequent Bark Beetle Outbreaks

The role of the spruce budworm as a predisposing factor for bark beetle outbreaks in western forests has often been assumed. It is more than likely that the weakening effect of budworm defoliation makes the host trees more susceptible to bark beetle attack. Apparently the point has never been tested, and therefore neither proven nor disproven.

Evenden (1933) in a report of experimental spraying against the budworm in Cody Canyon on the Shoshone National Forest, Wyoming, noted that the incidence of Douglas-fir beetle increased in seriously defoliated stands and that control operations against the beetle were necessary in the fall of 1931.

Bedard (1938) used the following notation to record the presence of the spruce budworm on Douglas-fir: "The spruce budworm has killed many trees in the Rocky Mountain region by completely defoliating them. Epidemics of this insect are usually followed by epidemics of the Douglas-fir beetle, which attacks and kills many additional trees."

Thomas (1958) made a critical study of bark beetle mortality of budworm-defoliated white spruce in the Lake Nipigon area of Ontario. He reported that the increased supply of weakened and dying white spruce trees provided by the budworm probably was a major factor permitting populations of the bark beetle Dendroctonus piceaperda to increase to destructive numbers from an endemic level. He indicated that outbreaks of this bark beetle may be a natural development in a spruce-balsam fir forest subjected to a severe outbreak of the spruce budworm.

#### DIAPAUSE IN THE SPRUCE BUDWORM

After eclosion, spruce budworm larvae normally construct hibernacula in suitable sites, molt to the second instar, and then enter a period of diapause. The diapause normally lasts from August until the following April or May. The second instar larvae then emerge from their hibernacula and begin feeding after the average daily temperature reaches about 60° F.

During the period in which the larvae are entering diapause and for a period of varying length thereafter, the larvae experience average daily temperatures considerably higher than that which will induce them to emerge the following spring. Both temperature and photoperiod appear to be involved in the inception and termination of diapause.

#### Inducement of Emergence of Overwintering Larvae

Cole (1958) was able to cause emergence of overwintering budworm larvae within 3 to 4 weeks by the following treatment:

(1) storing fall-cut billets at 32 to 40° F. for 1 week, (2) then storing the billets at -25° F. for 8 hours, and then (3) removing them to an insectary (60 to 70° F.) for emergence.

Harvey (1958) found that initial emergence of budworm larvae at 21° C. that had been stored 6 and 14 weeks at 0° C. was greater when they were subjected to photoperiods of 15 and 18 hours than for photoperiods of 0, 12, or 24 hours. The greatest number of larvae eventually emerged when they were exposed to continuous light in comparison with all other photoperiods. The effect of continuous light was not observed after a storage period of 20 weeks.

#### The Absence of Diapause

Harvey (1954) reported that nondiapause budworm stock was developed for laboratory cultures. The percentage of nondiapause larvae was 20.6 percent in the first generation and 38.5 percent in the second. Values as high as 80 percent were obtained. The length of generation was 2 months compared to 6 months for normal diapausing laboratory cultures.

After more intensive study, Harvey (1957) found in laboratory studies that in 62 percent of the families produced by matings of field-collected individuals at least one larva could develop without diapause if subjected to long photoperiods while being held at 71° F. He observed that on the average 3 to 4 percent of the second instar larvae of such progenies could forego diapause.

Selection over six generations yielded a strain that when subjected to continuous light in the laboratory was virtually free from diapause. The stock was reared for another six generations and still retained this characteristic.



Behavior of the nondiapausing larvae was normal during the period of hibernacula construction and molting, but the larvae then left the hibernacula and fed readily and developed normally. Mortality, mating success, and fecundity of this stock was not different from diapausing stock.

Harvey postulated that the ability to develop without diapause was determined by multiple genes; it was not sex-linked but might be sex-controlled to some extent.

#### Second Diapause in the Spruce Budworm

The occurrence of a second period of diapause in the life cycle of western budworm populations has been treated earlier under "Two-year-cycle budworm". Temperature appears to be the mechanism responsible for the inception of the second diapause.

By transferring experimental rearings of 1-year-cycle budworms to an area where the budworm normally has a 2-year-cycle habit, Campbell (Campbell, D. K., 1953) was able to convert the 1-year-cycle budworm to a 2-year habit. Prolonged development of the parents due to lower temperatures at higher elevations appeared to be the major factor involved. Three individuals of normally 2-year-cycle budworm developed in 1 year when they were reared in an area where wild populations normally had a 1-year life cycle.

Harvey (1961) observed a very low incidence of second diapause in laboratory and insectary rearings of spruce budworm from eastern Canada. The tendency to undergo a second diapause may be inherited and may also be induced by environmental factors.



### Hibernation Sites

The construction of a hibernaculum by a budworm larva appears to be a response to a tactile stimulus. The site in which the structure is constructed seems to depend considerably on the nature of the host and what is available in the way of "suitable" sites. The larvae have been reported to hibernate on the foliage, at the base of needles, under bark scales, in old Adelges galls (Cook 1949), on lichens and moss on tree trunks and limbs, in flower cups, and in mined buds (Batzner 1960). The proportion of larvae found on the bole of the tree is probably greater on tree species with coarser bark and larger bark scales compared to the smoother-barked species (Carolin 1950).

### DISPERSAL OF THE SPRUCE BUDWORM

Dispersal of the spruce budworm has been determined responsible for the spread of infestations from localized outbreaks. Susceptible forest composition, first, and climatic release, second, are the causes of population buildups in the outbreak centers.

The spruce budworm is susceptible to dispersal at three points in its life cycle. First and second instar larvae, while seeking hibernation sites or suitable food, respectively, become dislodged from the foliage and drop on silken threads. They may be caught in air currents and carried short distances. Adult moths may be caught in air currents and carried considerable distances.

### Larval Dispersal

Batzner (1962) found that the average velocity of fall of second instar budworm larvae, when compared with the length of their silk threads, exhibited a negative exponential relationship that was highly

significant. From this relationship, the dispersal distance can be estimated for any wind speed or height above the ground.

#### Dispersal of Budworm Adult Moths

In the Green River studies, Morris (1948) reported that 54 spruce budworm moths were taken in light traps in 1947. Of this total, 77 percent were males, 23 percent females. Male moths are more attracted to lights and fully gravid and spent females are sluggish and often incapable of active flight. Morris found mercury vapor lights to be more attractive than Coleman lanterns.

Greenbank (1950) recorded a large flight of moths from a heavily infested area into the Green River area on July 28, 1949. The ratio of moths caught in traps to pupal population per tree was 10 in 1947, 6 in 1948, and 12 in 1949 ignoring the moth flight and 140 taking it into account. Females constituted 20 percent of the catch and, by dissection, it was determined that they bore a mean egg complement of 70 eggs.

Light traps on forest lookout towers, supplemented by daily observation sheets, were found useful to detect large moth flights (Greenbank 1951). Large tanglefoot boards on the towers were also used. Light traps were not desirable in the forest stands because of the fire hazard and the frequent attention required. Virgin females, caged on tanglefoot boards, were found to be useful to trap males.

Greenbank (1957) concluded that, although New Brunswick budworm populations were increasing in 1947, the outbreak of 1949 was a

continuation of the spread of high populations across Quebec to the west. He observed that if the invading moths are deposited in dense, mature, softwood stands, outbreaks soon develop. If the moths are deposited in young, open, or mixed-wood stands, the resulting high populations do not succeed unless replenished by other invasions.

Henson (1951) reported his analyses of 19 mass flights of budworm moths. The mass flights always take place in the evening or early part of the night. The farther the point of deposition, the later at night the flight is observed. In some cases, the passage of a cold front followed deposition. In some cases, brief rain preceded the flight. The heavy evening flight is a response to light of decreasing intensity, the number of insects in flight being directly related to the rate of decrease of light. The insects were carried by convective storms which precede cold fronts. Prefrontal thunderstorms that cause a sudden reduction in light and also bring about pressure changes are responsible for initiation of mass flights.

A typical thunderstorm has a strong updraft in front of each cell, the wind blowing toward the storm. Insects drawn up into the storm may be tossed out at the top or sides of the cloud, deposited with rain in the central downdraft, or carried in the storm.

#### POPULATION DYNAMICS OF THE SPRUCE BUDWORM IN EASTERN CANADA

Morris et al. (1958) and Morris (1958) have reviewed the spruce budworm outbreak that lasted 10 years in the Green River study areas.

A few years of observations on the endemic condition were obtained before the outbreak began, and now the studies of the endemic conditions following the outbreak are continuing (Miller and Macdonald 1961; Miller 1962). Life tables based on intensive population sampling on permanent plots, complemented by data on fecundity, natural and applied control factors, and dispersion, have been constructed for consecutive generations in different forest types (Morris and Miller 1954).

It appears that a susceptible forest composition must be present before an outbreak can occur. Stand factors are the essential predisposing cause of outbreaks (Morris et al. 1958) and determine the average level of abundance of the budworm in different forest stands (Miller and Macdonald 1961). Weather and natural enemies largely determine the direction and extent of deviations from this average (Miller and Macdonald 1961).

The budworm is attacked by many parasites, but they are able to exert control only over low populations or in infestations where budworm population increases are not too rapid or sustained (Morris et al. 1958). Generally, they react to budworm population increases in a delayed manner and are unable to respond to rapid increases brought about by favorable weather in an extremely favorable forest type (Balch 1960).

Dispersal of budworm larvae can be a serious mortality factor where the forest stand is discontinuous or variable, but an invasion of partially gravid female moths can upset whatever delicate balance of control may be obtained by natural enemies (Morris et al. 1958).



## SAMPLING SPRUCE BUDWORM POPULATIONS

Investigations of spruce budworm populations have usually involved observations of a portion or sample of the population. It is seldom feasible to study an entire population. Each of the life stages of the budworm, egg, overwintering larva, feeding larva, pupa, and adult have been sampled, and different sampling techniques have been used by the various workers in different parts of the country. The techniques have necessarily differed depending upon whether the sampling was for study of the population dynamics of the insect in a relatively small area or the status of the insect was being estimated for a large area. Extensive sampling of a small area for population studies usually involves a considerable expenditure of time and effort to gain an accurate insight into the mechanisms responsible for population regulation. In survey sampling, some precision is often sacrificed to sample many more locations to determine population status on much larger areas.

Sampling of insect populations, including the spruce budworm, involves a measure of aggregation. Waters (1959) stated:

Aggregation is both a statistical and fundamental biological characteristic of insects and other animals. The aggregative behavior of nonsocial as well as social insects has a direct bearing on reproduction and survival and thus affects population dynamics and evolutionary trends. Owing to the distinct life stages of most insects, aggregation must be assessed throughout the entire life cycle.

Waters recommended the use of the smallest feasible natural unit for sampling, multiple or nested sampling, and stratification of



the data by population density and other meaningful criteria to increase the accuracy and reliability of estimates of  $k$ , a measure of aggregation.

The study of the population dynamics of the budworm for a long period of time on the Green River Watershed in New Brunswick involved a critical choice of sampling techniques. Morris (1955) described these techniques as follows:

The universe for which each life table is prepared is a homogeneous forest stand. It is shown that a collection unit smaller than a whole branch, or its longitudinal one-half, is unlikely to be suitable for the measurement of absolute population. Intertree variance is the major source of variance for the budworm, and for most other insects that have been studied intensively. Significant variance is also associated with crown levels, and the pattern of vertical distribution of the budworm is not predictable. The criterion of representativeness can be satisfied, however, by drawing samples from four crown levels in such a way that the intensity of sampling is equal in each level. The design found suitable for the budworm consists of proportionate sampling within the crown, stratified sampling by crown stories within the stand (with sub-strata, when necessary, according to host species or flowering condition), and cluster sampling within strata. Samples may be drawn from the same trees during successive budworm generations and show correlations which appear to arise from the preferences of ovipositing adults.

Other workers have chosen other collection or sample units as will be shown in the following discussions of sampling each of the life stages of the budworm.

#### Sampling the Egg Stage

The numbers of egg masses counted on different samples varies, of course, with the size of the samples. Morris (1949) described a method, which has been used with modification in some western areas (Carolin and Coulter 1959b), to take this variable into account.

He measured the length and the mid-point width of the foliated portion of each selected branch, the product of these measurements giving an approximation of branch surface area. He then expressed the egg mass density as "egg masses per 100 square feet" of foliage examined. He also used this method to compute the density of other life stages such as larvae and pupae. Carolin and Coulter (1959b) compute the branch surface by dividing by two the product of the foliated length and the width at the widest point of longitudinal half-branches. They express egg mass density as "egg masses per 1,000 square inches of foliage" examined.

Fettes (1949, 1951) used an egg mass index based on the number of egg masses per foliated twig on the assumption that each twig presents comparable oviposition opportunities. He found that female moths had no preference for old or new foliage as oviposition sites. He felt that his method eliminated variation due to the amount of foliage on the sample branches.

One purpose of determining egg mass density, particularly in survey work, is to predict the amount of defoliation that will occur the next season so that control activities may be planned. Webb (1958b) reported that in eastern Canada the probable degree of attack was predicted by the following regression: Probable percentage loss of new growth =  $0.27x + 5.8$  where  $x$  = the number of egg masses per 100 square feet of mid-crown branch area. He observed that in sprayed areas the loss was about 9 percent less than predicted the first year after spraying.

Morris (1954) developed a sequential sampling procedure for egg mass surveys in Canada. Infestations were classified as light, moderate, or severe.

Other sample units have been used to sample the egg and other stages. Dowden and Carolin (1950) utilized a technique of 15-inch samples taken from the terminals of mid-crown branches. Atwood (1944) used an 18-inch sample in insect surveys in Ontario.

Wilson (1959) developed a method of subdividing samples of any size to reduce the amount of foliage that had to be examined for egg masses. His technique consisted of separating the tips of the shoots from the rest of the branch and then increasing the numbers of egg masses on the tips by 16 percent to obtain the total for the branch. The method could be used on any size branch from any portion of the crown but could not be used on branches with severe or complete defoliation.

The density of the egg population is usually expressed in egg masses since it is quite time consuming to count individual eggs, and it is usually felt that the average number of eggs is quite constant. Bean (1961a) counted the number of eggs in 45 egg masses from balsam fir in each of three stand conditions. He found a distributional pattern such that he thought the use of an average number of eggs per mass undesirable in population studies. In his report, he presented a table based on the regression line showing the relationship between the number of eggs and egg-mass length.

In the preceding paragraphs, balsam fir has been the budworm host sampled. In the western United States, Douglas-fir is a preferred host, and the sampling method differs somewhat from those described above. Carolin and Coulter (1959b) have developed the techniques of sampling budworm populations in Oregon and other western areas and their findings are summarized below.

Carolin and Coulter found that either the lower or middle crown thirds could be used for sampling the egg population. Two longitudinal half-branches from each of five trees in each plot were examined. The branches were measured as previously described and branch areas computed. Sampling errors, expressed as percent of the mean, were found to be similar for total number of egg masses per branch and number of egg masses per 1,000 square inches of foliage area. Fifteen-inch twigs were least useful as a sample of egg mass density (Carolin 1950). The number of egg masses per 1,000 square inches of foliage are significantly correlated with the number of larvae per 100 fifteen-inch twigs attacking the buds.

Carolin and Coulter found no significant differences between the density of new egg masses and the density of old egg masses during the following year. Terrell (1961b), however, contends that old egg masses do not represent an accurate index of the preceding year's egg mass population due to the loss of many old egg masses during the first year. Fettes (1951) found a high loss of new egg masses during the period between deposition and eclosion.

Silver (1960), studying a budworm outbreak on Douglas-fir in British Columbia, did not consider egg mass density a reliable index



for subsequent defoliation. Harris and Edwards (1960) sampled 2-year-cycle budworm on alpine fir and white spruce in British Columbia. They compared egg mass densities on 3 branches and 18-inch twigs taken from 3 crown levels on each tree sampled. Branch direction did not affect the counts, but significantly fewer egg masses were found on the lower crown third compared to the mid- and upper-crown. The 18-inch twig sample was found to be as satisfactory as the whole branch. In the outbreak studied from 1958 to 1961, there were more eggs per mass in the relatively newly infested areas than in the older areas (Harris 1962).

#### Sampling Populations of Overwintering Larvae

Denton (1951) pointed out the advantages of being able to predict defoliation from counts of larvae forced from hibernation in the winter months or early spring before their natural emergence. When planning for control operations, it is desirable to be able to predict the need for control as close to the period of damage as possible. Predictions based on pupal or egg mass surveys the preceding summer do not include an estimate of overwinter mortality. Counts of overwintering larvae made in the early spring are more realistic because the overwinter mortality has taken place.

Miller and Terrell have presented techniques for sampling overwintering larval populations. Miller (1958) showed that the collection of balsam fir foliage samples in the spring and sampling the whole branch as a unit was an acceptable technique. Terrell (1959), working in Montana, caged field-collected bolts and



collected the emerging larvae. He pointed out that a sampling program must consider these points: (1) samples collected from north or south slopes yield higher populations than samples from valley bottoms, (2) hibernating larvae are more numerous per unit of bark surface on tree boles than on limbs, (3) five bole sections are required from each sampling point for an adequate sample.

Carolin (1950) concluded that hibernating populations on the trunk and limbs, when expressed on the basis of larvae per 100 square inches (of bark surface?), provide a reasonable index to subsequent feeding populations, on the basis of the branch whorl.

#### Sampling Populations of Feeding Larvae

In the early Green River studies, larval sampling involved the examination of the top 5 feet of mature spruce and balsam fir trees recently felled for pulpwood (Balch 1945).

Fettes and Morris pointed out that because budworm larvae prefer new shoots as food, larvae per new shoot or bud was the most appropriate index of larval density (Fettes 1951; Morris 1955). Morris, however, retained his method of expressing insect density as individuals per 100 square feet of foliage surface.

Fettes (1951) obtained his branch samples from the flowering portion of balsam fir trees, the number of samples examined depending on the variation within the stand.

Cook (1949) used 18-inch twigs to sample populations of 2-year-cycle budworm. Twigs of this size gave an accurate estimate of the second-year feeding larval populations on the whole branch (Harris

1962). Atwood (1944) used the 18-inch twigs to sample needle mining populations of the budworm.

Bean has described two indirect methods of sampling larval populations. One is based on the assumption that the number of maggots of a group of Dipterous parasites falling on a unit area of ground will be an index of the budworm populations on the tree above that area (Bean 1957 and 1958b). The other method makes use of the correlation of frass width, but not its length or volume, with the various larval instars (Bean 1958a and 1959). Field-collected frass can be used as an index of the percent of larvae in each instar present when the collection was made.

Fifteen-inch twigs have been used by western entomologists to sample populations of budworm larvae on Douglas-fir and alpine fir (Cole 1958, 1960a, and 1960b; Chansler 1960; Carolin and Coulter 1959b). The sample unit used by Cole (1958) consisted of four 15-inch twigs, one terminal and three laterals, from the mid-crown of each tree sampled. He found a significant difference in the distribution of both larval populations and defoliation between trees of different ages. This difference existed between the mature-sapling reproduction and the immature-pole-age classes. He found no significant population variation between the second through the fifth instars but a significant difference between these stages and the last two, the sixth and pupal (Cole 1960b). Cole (1960a) presented sequential sampling plans for precontrol sampling or appraisal survey and for post-control sampling.

Sampling Douglas-fir in Oregon, Carolin and Coulter (1959b) concluded that to establish area-wide damage relationships, larval populations should be expressed on the basis of the number of larvae per 1,000 buds, rather than larvae per 100 fifteen-inch twigs. Using plot averages, they found the relationship of larval populations per 1,000 buds to percent defoliation of current growth to be highly significant.

#### Sampling Populations of Pupae

Fettes (1951) and Morris (1955) expressed the density of pupae in the same manner as larval populations. Western workers generally use the 15-inch twig to sample pupal populations.

Terrell (1961b) uses the density of the pupal population as an index to the moth population by sampling after the moths have emerged and counting the empty pupal cases. He found that the moth population correlates with subsequent defoliation, but moth flight or the invasion of moths from other areas can make estimates of defoliation invalid.

#### Estimates of Defoliation

It is generally agreed that estimates of defoliation are useful indices of past budworm activity (Fettes 1951; Terrell 1961b). An estimate of current defoliation is not a valid means of predicting the trend of the outbreak, however (Terrell 1961b).

Fettes (1951) and Terrell (1961a) reported methods of estimating current defoliation from collected branch samples. Fettes trained observers to grade any new growth shoot according to one of 13

standards, corresponding to categories of percent defoliation, which the observers had been trained to recognize. Terrell (1961a) found a consistent relationship between the number of undamaged shoots and the percent defoliation. He utilizes counts of undamaged shoots to estimate defoliation.

Carolín and Coulter (1959b) found that visual estimates of percent defoliation on individual trees based on field glass estimates for each crown third to be related to the density of larval populations on these trees. Their method of weighting the estimates for each crown third by the proportional amount of foliage in each improved the relationship. Other workers have used field glass estimates for only the mid-crown and believe that they do not differ from estimates based on weighted estimates of each crown third. Carolín and Coulter found that estimates based on shoot tallies for the middle crown third to be not closely related to larval densities on the trees, but they feel that such estimates give a better estimate of defoliation and bud killing for the plot than do field glass estimates. The incidence of bud killing is not directly related to the population level or to percent defoliation but is an important damage factor.

Silver (1960) used field-glass estimates to determine current defoliation on Douglas-fir in British Columbia. By using his unpublished data showing that current growth constitutes 20 to 30 percent of the total foliage on a tree, he was able to estimate total defoliation, also. Fettes (1951) found, on trees sampled in 1946, that 18.2 percent of the foliage developed in 1945.



### Aerial Surveys of Spruce Budworm Damage

The airplane has been used by observers to detect and delineate spruce budworm outbreaks in all areas where the insect causes extensive damage. Heller et al. (1952), Waters et al. (1958), Schmiede (1958), and Heller and Schmiede (1962) have reported research to improve aerial surveys. Spruce budworm infestations have been delineated by aerial observers since 1956 in the Central and Southern Rocky Mountain Region.

### CHEMICAL CONTROL OF THE SPRUCE BUDWORM

#### Insecticide Evaluation

In 1930, the Deficiency Bill of the Bureau of Entomology carried a request for \$10,000 for experimental control with arsenicals of the spruce budworm in Cody Canyon, Shoshone National Forest, Wyoming (Anonymous 1930). Evenden (1933) reported that the sprays applied in the 1931 operation were not much more effective than the natural control that occurred on untreated trees. The end of the outbreak was predicted in both 1930 and 1931. Defoliation was worse in 1932 than the year before, and about the same on treated and untreated trees. Lead arsenate was used in these tests.

Orr and Wygant (1945) reported insecticide tests near Estes Park, Colorado, using a large power sprayer. DDT at one-half pound or more per 100 gallons of water or about 2½ pounds or more per acre caused almost complete budworm mortality on Douglas-fir and spruce and was nearly as effective on pine. The best results were obtained by spraying just before the larvae left their hibernacula,



but applications during feeding periods gave satisfactory results. Adult moths were readily killed by DDT. None of the lead arsenate formulations were as satisfactory as DDT.

Brown et al. (1947) tested 15 organic insecticidal compounds for their direct contact toxicity to larvae of Agrotis orthogonia, Heliothis ononis, and Choristoneura fumiferana. The compounds, dissolved in a benzene/kerosene mixture, were applied at graded concentrations in a spray tower. The pyrethrins, gammexane, and DNOC were among the four most toxic compounds to all three species. DDT was highly toxic to H. ononis and C. fumiferana. Rotenone and Texaphene were moderately toxic to all three species.

In 1953, Elliott et al. (1954) compared BHC and an organic phosphate with DDT in hand sprayer, mist blower, and aerial tests. DDT at 1 pound per gallon and applied at 1 gallon per acre, produced the best results. The choice of solvents appeared to be of little or no importance in terms of budworm mortality.

Smith (1954) reported tests in New Brunswick to compare four insecticides with DDT for small ground-spraying projects. The tests indicated that Malathion was almost as effective as DDT, and since it also killed mites it was considered a suitable substitute for DDT for use on shade trees. Lead arsenate was only moderately effective, and both Aldrin and Dieldrin gave poor results.

After testing the action of DDT on newly hatched budworm larvae, Smith (1955) decided that residual action is likely to be of little importance. He found the residual effect of DDT to last only 1 or 2 weeks, and budworm egg hatch takes place 6 to 8 weeks after application.

Secrest and Thornton (1959) found DDT to be superior in tests involving DDT, BHC, Aldrin, Dieldrin, and Endrin at normal and quarter strengths.

Malathion was shown to be an effective insecticide when compared with DDT in a pilot control test in southern Colorado in 1962 (Wilford 1962b). This was the first use of Malathion in a budworm control project in the western states. The insecticide has a lower mammalian toxicity and shorter residual than DDT.

Randall (1962) reported laboratory tests involving three systemic insecticides--dimethoate, menazon, and phosphamidon. As measured by budworm larval mortality, dimethoate and phosphamidon were effectively translocated in white spruce seedlings.

Nagel (1962) demonstrated that dimethoate and DDT prevented damage by budworm larvae to buds on Douglas-fir of Christmas-tree size. Dimethoate was as effective as DDT at twice the emulsion concentration. The translocation of dimethoate was not demonstrated because of late application, but the larvae were killed by wetting the needles.

#### Aerial Spraying for Spruce Budworm Control

Control of the budworm in the United States and Canada by aerial application of insecticides usually consists of large projects involving several agencies, many individuals, much equipment, and large forest areas. Precise timing of the application is necessary to obtain the desired results, and cooperation among individuals and agencies is of great importance. General treatments of the history, techniques, and problems of aerial spraying for budworm control

include those by Morris (1951b), Balch (1952), Webb (1955a, 1955b, 1958a, 1959, 1960), Terrell (1956), Fettes (1956), Blais and Martineau (1960), Denton (1960a), Webb et al. (1961), Blais (1961), and Bean (1961c).

Swaine (1930) gave detailed accounts of airplane dusting for budworm control in Ontario in 1929. At least 30 to 40 pounds of calcium arsenate dust per acre were required. The approximate total cost per acre was about \$6.

Eaton et al. (1949) described 1948 tests on airplane and helicopter spraying with DDT in eastern Oregon. This was the first demonstration of the effectiveness of DDT sprays against high budworm populations, with practical spraying procedures that would be used on an actual operation. Excellent control was obtained with both 1 pound of DDT in 1 gallon of fuel oil per acre and 2 pounds of DDT in 2 gallons of fuel oil per acre. The application of one-half pound of DDT in one-half gallon of fuel oil per acre by helicopter gave unsatisfactory control. Also, the 1-pound applications by helicopter gave lower, but satisfactory, mortalities than did the applications by plane. The sprays were applied when the larvae were actively feeding on the foliage.

Davis et al. (1956) tested different atomizations, dosages, and stages of budworm development to determine the best combination of these factors. They concluded that maximum kill would be attained if treatment was made when most of the larvae were in fourth and fifth instars. The minimum dosage of DDT for maximum kill was 1

pound of DDT per acre. A spray of medium atomization (150 microns mass median diameter) gave the most consistent effective results.

Davis et al. (1957) described tests conducted in 1956 in Montana and Idaho to determine if the spray height for large planes could be raised from the 200 to 400 feet that was being recommended. Six blocks of 2,500 to 6,000 acres each were sprayed, 2 at 250 feet, 2 at 500 feet, and 2 at 750 feet. Lowest variability in budworm mortality and greatest insecticide deposit were obtained at 750 feet. These results prompted a more critical evaluation of the 750-foot height in 1957 (Davis et al. 1958) on a 30,000-acre area. Low budworm mortality (average 89.1 percent) was attributed to low intensity of infestation, late application, and irregularities in flight line spacing and deposit distribution. Due to this marginal control, the adoption of the 750-foot height was not recommended.

#### Hazards to Birds and Fish

The application of DDT to large forest areas has been considered a possible hazard to insectivorous birds. George and Mitchell (1947), after laboratory and field tests, concluded that if nestlings were fed both treated and untreated insects, they would not die. If the dosage of insecticide was sufficient to cause complete mortality of the budworm larvae, some nestlings would probably die due to poisoning or a combination of poisoning and weakness because of lack of food.

Extensive killing of young salmon occurred in 1957 on Vancouver Island and in New Brunswick after applications of DDT at the rate of



1 pound and one-half pound per acre, respectively (Fettes 1960; Fettes and Randall 1962). Fettes (1960) reported aerial spray trials to evaluate other insecticides less toxic to fish. DDD, Korlan, Sevin, and Malathion (at one-quarter and one-eighth pound per acre) were not as effective as DDT against the budworm. DDT was found to be effective at 1, one-half, and one-quarter pounds per gallon of formulation per acre where coverage was adequate.

In 1960, part of the control program in New Brunswick included a large portion of the area sprayed with one-fourth pound of DDT per acre, and in 1961 this dosage was used for the entire program (Fettes and Randall 1962). The lower dosage is less toxic to fish and aquatic insects.

Phasphamidon, the systemic insecticide, has been found to be only one-fortieth as toxic as DDT to young Atlantic and Pacific salmon and shows considerable promise for forest spraying (Fettes and Randall 1962).

#### SILVICULTURAL CONTROL OF THE SPRUCE BUDWORM

Spruce budworm control by forest management has been recommended for balsam fir stands. As early as 1923, Craighead (1923) made three recommendations for control of epidemics: (1) diversified types to break up continuous canopies of balsam fir; (2) utilization of hardwoods to encourage mixed softwood-hardwood types; and (3) short rotations of all balsam fir mixtures and pure spruce in the vicinity of balsam fir.



Atwood (1945) pointed out the need for standards to estimate the susceptibility and vulnerability of any given stand to budworm attack. Pulpwood operators needed to know which stands were in immediate danger and which were relatively safe so they could plan their cutting operations. Foresters and entomologists were interested in detecting areas that would be particularly susceptible and serve as foci for outbreaks. Balch (1946) presented a map showing the relative susceptibility of different areas in the Northeast with recommendations for management.

It was agreed that an accumulation of mature balsam fir was necessary for a budworm outbreak and cutting practices were recommended to remove such accumulations. Heimburger (1945) apparently interpreted this as an artificial change in species composition "preferably by almost completely eliminating balsam fir." He was convinced that this treatment would be unsuccessful and discussed the value of tolerant hardwood barriers and their location by biogeographical considerations.

Management plans and risk-rating systems for selective cutting were presented by Westveld (1946, 1954), McLintock and Westveld (1946), and McLintock (1948, 1949) for the Northeast. Bean and Batzer (1956) used a risk-rating system in the Lake States based on density, age, composition, area, and vigor of spruce-fir types.

Graham (1951) discussed forest management for control of various insects, including the spruce budworm.

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